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**A re-evaluation of the Plenus Cold Event, and the links between CO<sub>2</sub>, temperature,  
and seawater chemistry during OAE 2**

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**Key Points:**

- This study is the first to review mechanistic interactions, and temporal leads and lags, between temperature, seawater chemistry, and CO<sub>2</sub> within the Plenus interval
- The negative carbon-isotope excursion during the Plenus interval was a global event driven by a CO<sub>2</sub> increase, and appears decoupled from cooling and circulation changes
- Cooling was not globally synchronous; local climatic & environmental responses to the CO<sub>2</sub> change are more complex than previously understood

**Abstract**

The greenhouse world of the mid-Cretaceous (~94 Ma) was punctuated by an episode of abrupt climatic upheaval: Oceanic Anoxic Event 2 (OAE 2). High-resolution climate records reveal considerable changes in temperature, carbon cycling, and ocean chemistry during this climatic perturbation. In particular, an interval of cooling has been detected in the English Chalk on the basis of an invasive boreal fauna and bulk oxygen-isotope excursions registered during the early stages of OAE 2—a phenomenon known as the Plenus Cold Event (PCE), which has tentatively been correlated with climatic shifts worldwide.

Here we present new high-resolution neodymium-, carbon-, and oxygen-isotope data, as well as elemental chromium concentrations and cerium anomalies, from the English Chalk exposed at Dover, UK, which we evaluate in the context of >400 records from across the globe. A negative carbon-isotope excursion that correlates with the original ‘PCE’ is consistently expressed worldwide, and CO<sub>2</sub> proxy records, where available, indicate a rise and subsequent fall in CO<sub>2</sub> over the Plenus interval. However, variability in the timing and expression of cooling at different sites suggests that, although sea-surface paleo-temperatures may reflect a response to global CO<sub>2</sub> change, local processes likely played a dominant role at many sites. Variability in the timing and expression of changes in water-mass character, and problems in determining the driver of observed proxy changes, suggest that no single simple mechanism can link the carbon cycle to oceanography during the Plenus interval and other factors including upwelling and circulation patterns were locally important. As such, it is proposed that the Plenus carbon-isotope event is a more reliable stratigraphic marker to identify the Plenus interval, rather than any climatic shifts that may have been overprinted by local effects.

## 1 Introduction to Oceanic Anoxic Event 2 and the Plenus Cold Event

At a global scale, the latest Cenomanian–earliest Turonian interval was characterized by the most significant environmental perturbation of the Late Cretaceous: Oceanic Anoxic Event 2 (OAE 2; Schlanger & Jenkyns, 1976; Arthur et al., 1990; Jenkyns, 2010). OAE 2 was an interval of extreme greenhouse conditions, with high temperatures and high atmospheric  $p\text{CO}_2$  (Arthur et al., 1988; Jenkyns et al., 1994; Kuypers et al., 1999; Jarvis et al., 2011; O’Brien et al., 2017). The leading hypothesis for the initiation of the OAE invokes the submarine emplacement of large igneous provinces releasing vast quantities of  $\text{CO}_2$  into the ocean and atmosphere, leading to an intensified greenhouse climate that caused an accelerated hydrological cycle and enhanced nutrient flux to the oceans (e.g. Jenkyns, 2003). Volcanism and/or other types of basalt–seawater interaction may also have supplied biologically significant metals directly into seawater (Orth et al., 1993; Snow et al., 2005; Turgeon & Creaser 2008; Du Vivier et al., 2014; Jenkyns et al., 2017). Nutrient input is credited with enhancing organic productivity on a global scale, increasing the carbon flux to the sea floor to form the characteristic black-shale record and a distinctive positive  $\delta^{13}\text{C}$  excursion—together constituting the hallmark of the OAE—as well as progressively leading to significant regional deoxygenation in many parts of the world ocean, particularly the North Atlantic (e.g. Pearce et al., 2009; Jenkyns, 2010). Bottom-water anoxia and hypoxia possibly affected 40–50% of the global ocean, but with euxinic (sulphidic) bottom waters affecting a much smaller percentage (Monteiro et al., 2012; Owens et al., 2013; Dickson et al., 2016, 2017; Ostrander et al., 2017).

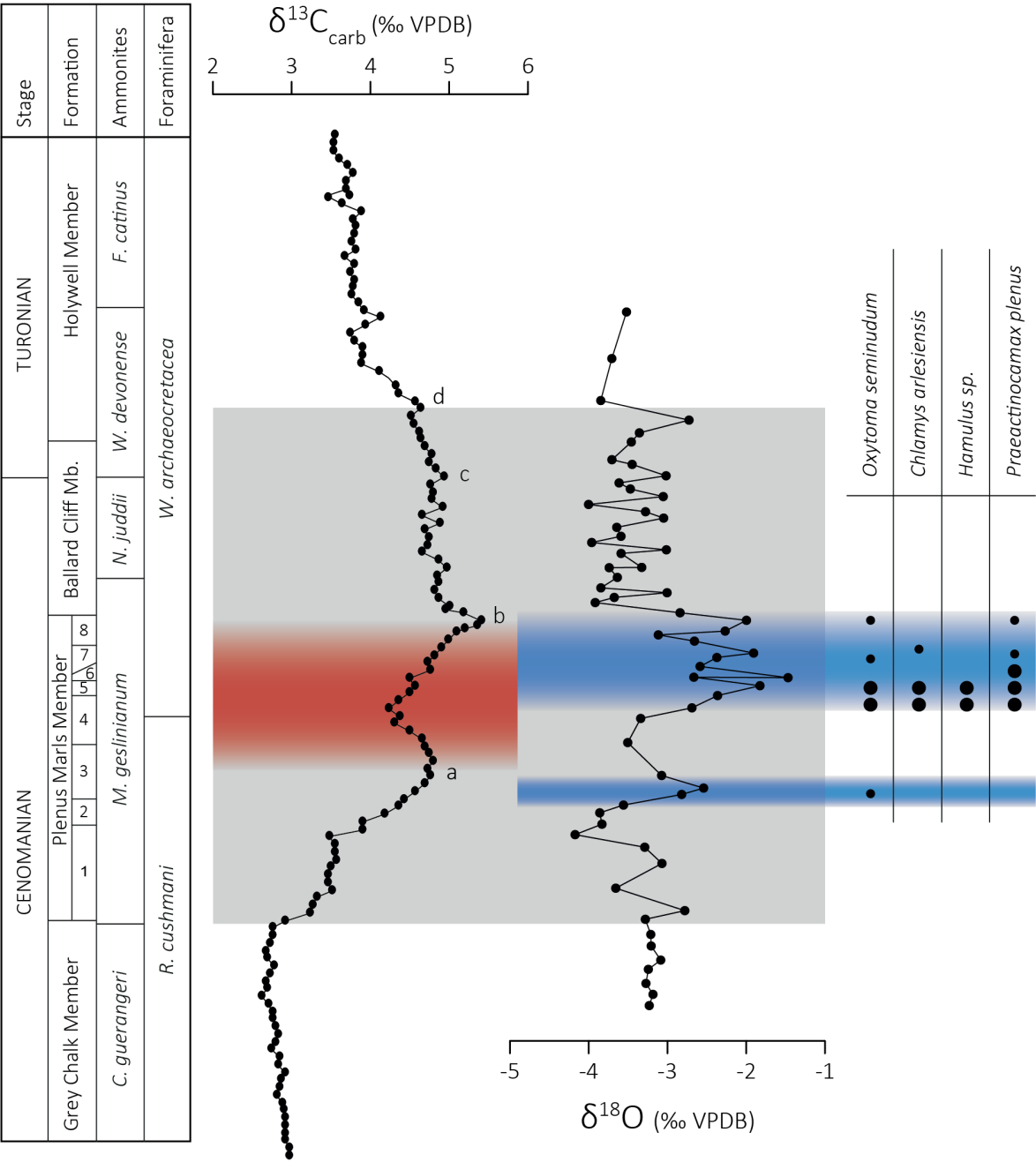
Accelerated burial rates of planktonic organic matter, whose biosynthesis led to preferred incorporation of the lighter  $^{12}\text{C}$  isotope, resulted in a marked positive carbon-isotope excursion recorded in different sedimentary archives around the world (e.g. Scholte & Arthur 1980;



Schlanger et al., 1987; Jenkyns et al., 1994; Tsikos et al., 2004; Bowman & Bralower 2005; Voigt et al., 2006; Jarvis et al., 2011; Wendler, 2013). The canonical model suggests that, eventually, increased rates of organic-carbon burial would have caused a drawdown of atmospheric CO<sub>2</sub>, ultimately triggering global cooling that led to a weakening of the factors promoting carbon burial (Arthur et al., 1988; Jenkyns et al., 1994; Kuypers et al., 1999; Sinninghe Damsté et al., 2010; van Bentum et al., 2012; Gale et al., 2019).

Lithium- and calcium-isotope records suggest that, in addition to organic-carbon burial, enhanced silicate weathering in both subaerial (under conditions of an accelerated hydrological cycle) and submarine environments during the OAE may have aided in the drawdown of CO<sub>2</sub> and the termination of the OAE (Blättler et al., 2011; van Bentum et al., 2012; Pogge von Strandmann et al., 2013; Jenkyns et al., 2017; Jenkyns 2018). However, it has recently been argued that the persistence of high temperatures globally throughout the latter stages of OAE 2 and into the early Turonian suggests that CO<sub>2</sub> did not decline, and that some other mechanism was responsible for the termination of the event, rather than a cessation of climatic factors favourable for ‘black shale’ formation (Robinson et al., 2019).

While the sedimentary expression of the OAE 2 interval varies worldwide, the carbon-isotope evolution of OAE 2 is broadly similar in all investigated sites across the world where the stratigraphic record is tolerably complete (Figure 1): first build-up, trough, second build-up, plateau with spikes, followed by decay towards background (Paul et al., 1999; Tsikos et al., 2004; Wendler 2013).



**Figure 1.** The composite ‘type-section’ recording OAE 2 and the Plenus Cold Event from the English Chalk, using  $\delta^{13}C_{carb}$  from Eastbourne (Tsikos et al., 2004), and bulk  $\delta^{18}O$  and boreal fauna from Dover (Lamolda et al., 1994; Gale and Christensen, 1996), correlated using the beds of the Plenus Marl Member (for details see Jarvis et al., 2006). Points ‘a–d’ show globally

consistent positions on the  $\delta^{13}\text{C}$  curve (Jarvis et al., 2006). The gray box shows the interval of OAE 2 (Jenkyns et al., 2017) extending from the uppermost Cenomanian to the lowermost Turonian. The red bar indicates the Plenus carbon-isotope excursion, as defined in this study. The blue bars indicate cooling, with the upper bar defined in this study as the PCE *sensu stricto* (Gale and Christensen, 1996).

In the early stages of OAE 2, between peaks ‘a’ and ‘b’ (Figure 1), a brief (~40 kyr; Jarvis et al., 2011) interval of cooling occurred that was first recognized in the chalk of the Anglo-Paris Basin by the southerly incursion of boreal fauna (notably the belemnite *Praeactinocamax plenus*) into the paleo-European mid-latitudes (Jefferies 1962, 1963). This interval was later discovered to be coeval with a positive oxygen-isotope excursion, and it was found that the spread of Boreal fauna extended southwards into the Tethys (southern France: Gale & Christensen 1996). This period of cooling was termed the ‘Plenus Cold Event’ (PCE) after the Plenus Marls, a relatively clay-rich interval in the English Chalk where the fall in temperature is registered (Figure 1; Jenkyns et al., 2017). Cooling during OAE 2 has been identified from a number of SST proxies from marine sections across the Northern Hemisphere (e.g. Forster et al., 2007; Sinninghe Damsté et al., 2010; Jarvis et al., 2011; Desmares et al., 2016; van Helmond et al., 2016; Gale et al., 2019), suggesting that the entire North Atlantic Ocean and its surrounding epicontinental seas were affected. Broadly synchronous with the PCE, a period of extensive bottom-water re-oxygenation occurred throughout the Western Interior Seaway of North America and the North Atlantic (Eicher and Worstell, 1970; Eicher & Diner, 1985; Leckie, 1985; Keller and Pardo, 2004; Forster et al., 2007; Friedrich et al., 2006; Keller et al., 2008; Eldrett et al., 2014; Zhou et al., 2015). The strata affected by re-oxygenation have been referred to as pertaining to the

111 'Benthic Oxidic Zone', although this event is typically equated with the Plenius Cold Event (e.g.  
112 Eldrett et al., 2014; van Helmond et al., 2016; Jenkyns et al., 2017), suggesting a global forcing  
113 mechanism for both climatic and redox changes.

114 Many authors have attributed the PCE to a decline in atmospheric  $p\text{CO}_2$  (e.g. Barclay et al.,  
115 2010; Sinninghe Damsté et al., 2010; Jarvis et al., 2011; Gale et al., 2019), suggesting that the  
116 transient negative  $\delta^{13}\text{C}$  excursion signifies reduced global burial of organic carbon under more  
117 oxygenated conditions, recorded at sites around the world (Erbacher et al., 2005; Voigt et al.,  
118 2008; Jarvis et al., 2011; Hasegawa et al., 2013). Estimates of the magnitude of the atmospheric  
119  $p\text{CO}_2$  decrease during OAE 2 range from 20–25% (Freeman & Hayes 1992; Jarvis et al., 2011)  
120 to 40–80% (Kuypers et al., 1999). Ongoing volcanism and/or basalt–seawater interaction during  
121 the early part of OAE 2 and the resultant input of greenhouse gases to the atmosphere is thought  
122 to have counterbalanced the carbon drawdown, maintaining relatively high temperatures except  
123 during the onset of the PCE, ultimately allowing the return to greenhouse conditions only when  
124 the rate of carbon dioxide supply exceeded the rate of its sequestration (Jenkyns et al., 2017).  
125 While a causal relationship has been postulated between carbon-cycle dynamics and cooling  
126 during the Plenius interval (e.g. Kuypers et al., 1999; Forster et al., 2007; Sinninghe Damsté et  
127 al., 2010; Jarvis et al., 2011), the existing records are from widespread locations and, as such,  
128 explanations of the PCE are sensitive to the stratigraphic correlation between sites.  
129 Understanding the timing of paleoenvironmental changes, both local and global, is therefore  
130 critical for disentangling the driver of climate change during this perturbation of the carbon  
131 cycle. As such, we seek here to investigate the synchronicity of environmental changes at the  
132 location where the PCE was first recognized, and to contextualize these data by synthesising all

available records to investigate the global responses of carbon-cycling, temperature, and seawater chemistry around the time of the PCE.

## 2 Materials and Methods

### 2.1 Plenus Marls, Dover

This study was conducted on the ~3 m thick Plenus Marls section near Shakespeare Cliff (Dover, UK; Figure 1), a well-known section for the study of OAE 2 (Schlanger et al., 1987). This site was located at a paleolatitude of ~42°N during the OAE (Van Hinsbergen et al., 2015), within the main part of the Anglo-Paris Basin. Across the basin, the Plenus Marls generally consist of a discrete unit of clay-rich chinks sandwiched between clay-poor chinks; the section at Dover comprises rhythmically bedded chinks and marls, rich in planktic foraminifera, nannofossils, macrofauna and clays (Jefferies 1962, 1963; Jeans et al., 1991). Jefferies (1962; 1963) introduced a numbering system for these beds (numbered 1–8), which has been generally adopted and followed in this study. The Shakespeare Cliff exposure at Dover is one of the best onshore sections for geochemical studies, as there has been relatively little diagenetic alteration of the chalk (Scholle et al., 1974). Previous studies argued that, although foraminiferal  $\delta^{18}\text{O}$  had been lowered by burial diagenesis, the relative trends were still reliable for paleoclimatic interpretation (Corfield et al., 1990; Jeans et al., 1991; Jenkyns et al., 1994; Lamolda et al., 1994).

The Plenus Marls were deposited in an epicontinental pelagic shelf sea during a major transgressive phase (Hancock 1993). During the mid-Cretaceous, this location was connected

with the Boreal Sea to the north, the Tethys to the south, and the North Atlantic to the west (Hancock 1975; Hancock & Kauffman 1979).

## 2.2 Sampling and sample preparation

Samples were collected every 10 cm from above and below the erosional base of the Plenus Marls up to Bed 8, with two additional samples at a 30 cm spacing from the overlying chalk. Samples were oven-dried for 48 hours at 40°C to remove residual water and the edges were scraped clean using a metal spatula to remove any loose rock debris or other detritus. Samples were then ground to a fine powder using an agate pestle and mortar, and homogenized.

## 2.4. Stable carbon and oxygen isotopes

Bulk carbonate samples were oxidized to remove organic matter by means of H<sub>2</sub>O<sub>2</sub> (15%, pH 8) being added to each sample and allowed to react for 30 minutes, then oven-dried at 40°C. Measurements were performed on a Delta V Advantage isotope mass spectrometer fitted with a Gas Bench II in the Department of Earth Sciences (University of Oxford); the carbonates were converted to CO<sub>2</sub> with 100% H<sub>3</sub>PO<sub>4</sub>. Three internal standards were used that have previously been calibrated to international reference materials: CarreraCam, Wiley, and NOCZ (n = 2, 2, 5 respectively). Respective  $\pm 1\sigma$  values are 0.04, 0.02, and 0.03‰ for  $\delta^{13}\text{C}$ , and 0.02, 0.07, and 0.02‰ for  $\delta^{18}\text{O}$ . In-house marble standard NOCZ has a long-term external repeatability of 0.07‰ for  $\delta^{13}\text{C}$  and 0.09‰ for  $\delta^{18}\text{O}$ .  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values are expressed in per mil variations relative to VPDB.

## 2.5. Neodymium isotopes

Nd was extracted from bulk chalk using the method of Zheng et al. (2013), followed by the standard two-stage ion-exchange column separation technique (Pin & Santos Zalduegui

1997). In short, 20 ml of 10% acetic acid was added to 5 g of powdered sample, and allowed to react for 2 hours. The samples were centrifuged, after which the supernatant was pipetted off, dried down, re-dissolved in 6 M HCl and dried down again, and finally re-dissolved in 1 M HCl before column chemistry. Rare-earth elements were separated from major cations using 0.8 mL AG50W-X12 (200–400  $\mu\text{m}$ ) resin with 6M  $\text{HNO}_3$  as an eluent. On a second column, Nd was separated from other REEs using 125  $\mu\text{l}$  of Ln spec (20–40  $\mu\text{m}$ ) resin with 0.25M HCl as an eluent.

Nd isotopes ( $\epsilon_{\text{Nd}(t)}$ ) were analysed on an MC-ICP-MS (NuPlasma) in the Department of Earth Sciences (University of Oxford). Mass bias was corrected by using  $^{146}\text{Nd}/^{144}\text{Nd} = 0.7219$  with an exponential law. Samples were measured by bracketing with the JNdi-1 Nd isotope standard, and the instrument drift was corrected by normalizing  $^{143}\text{Nd}/^{144}\text{Nd}$  ratios of the bracketing JNdi-1 to a reference value of 0.512115 (Tanaka et al., 2000). Total procedural blanks yielded  $\leq 355\text{pg}$  Nd, which is negligible compared to the minimum sample yield of 27 ppb Nd (sample DPM 140). The JNdi-1 standard had an external long-term reproducibility of  $\sim 0.4 \epsilon_{\text{Nd}}$  ( $2\sigma$ ), without application of a drift correction.

## 2.6. Chromium and rare-earth element concentrations

Approximately 0.01 g of the bulk carbonate sample was dissolved in 0.5 M acetic acid. The solutions so produced were subsequently dried down and re-dissolved in 2%  $\text{HNO}_3$  to form a solution containing approximately 100 ppm Ca. Standard solution mixtures containing a suite of synthetic standards of 40 trace elements including chromium and the rare-earth elements (REE) and doped with 100 ppm Ca were used to produce a calibration curve. Cr, Ce, Pr, and Nd concentrations were measured on an Agilent 7500s ICP-QQQ-MS at the Open University in  $\text{O}_2$  and He collision mode, respectively. Cerium concentrations were normalized to post-Archaeon

Australian Shale (PAAS) concentrations (Taylor and McLennan, 1985). Cerium anomalies are expressed as  $Ce/Ce^* = (Ce_{sample}/Ce_{PAAS}) / [(Pr_{sample}/Pr_{PAAS}) * (Pr_{sample}/Pr_{PAAS}) / (Nd_{sample}/Nd_{PAAS})]$  (Tostevin et al., 2016). Measurements are reproducible within 2% for Cr and 9% for Ce/Ce\* based on replicate analyses of JDo-1 (a carbonate standard reference material).



### 3. Results

#### 3.1. Stable carbon and oxygen isotopes

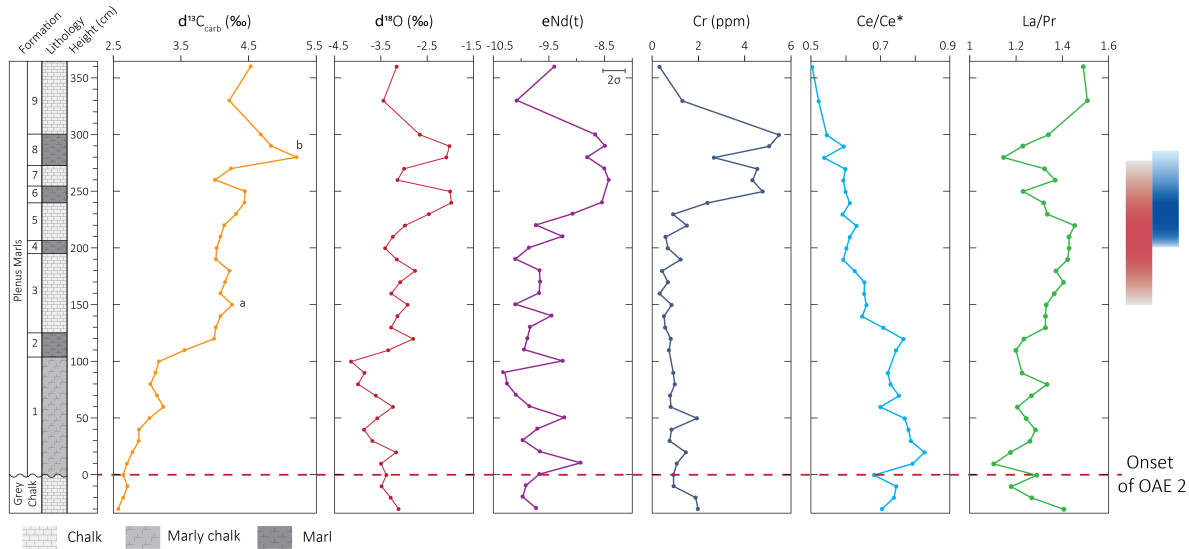
$\delta^{13}\text{C}_{\text{carb}}$  ranges from 2.57–5.21‰ (Figure 2), with a minor negative excursion at the level of the lower–middle part of Bed 7 in the Plenus Marls. The record shows positive shifts at Beds 2 (peak ‘a’) and 8 (peak ‘b’), though the trough between Beds 4 and 8 is not well expressed. The excursion documented here corresponds to excursions seen in other  $\delta^{13}\text{C}_{\text{carb}}$  records from Dover and Eastbourne (Jarvis et al., 1988; Jeans et al., 1991; Lamolda et al., 1994; Gale & Christensen 1996; Paul et al., 1999; Tsikos et al., 2004; Gale et al., 2005; Voigt et al., 2006; Pearce et al., 2009; Zheng et al., 2016).

The new Dover record shows  $\delta^{18}\text{O}$  varying between -4.14 and -1.98‰ with a positive shift at Bed 2 and a more significant positive excursion across Beds 6–8 characterized by a double peak indicating two phases of relatively greater  $\delta^{18}\text{O}$  values, which coincide with the main marls (Figure 2).

#### 3.2. Neodymium isotopes

Thirty-five samples had sufficient neodymium concentrations to allow measurement of Nd isotopes, which ranged from -10.3 to -8.4  $\epsilon$  units (Figure 2). This record shows a well-resolved 1.5  $\epsilon$  unit positive excursion, synchronous with the main cooling event, suggesting a change in water-mass chemistry in the Chalk Sea across southern England in the latest Cenomanian. The timing and magnitude of the positive excursion correlates well with the  $\epsilon_{\text{Nd}}$  record from Eastbourne; however, the new data do not show the earlier negative excursion recorded in Beds 2–4 at Eastbourne (Zheng et al., 2013), possibly owing to the presence of hiatuses and condensed horizons in the Dover section (cf. Gale et al., 1993; Jarvis et al., 2006). In a previous study of the Plenus Marls at Eastbourne, fish debris and bulk carbonates from the same stratigraphic levels

were found to record nearly identical  $\epsilon_{\text{Nd}(t)}$  values (Zheng et al., 2013, 2016). As such, the  $\epsilon_{\text{Nd}(t)}$  record here is interpreted dominantly to reflect bottom-water values.



**Figure 2.** New geochemical data from the Plenus Marls at Dover, UK. Points 'a' and 'b' are identified on the  $\delta^{13}\text{C}$  curve. With the exception of  $\epsilon_{\text{Nd}}$ , error bars are smaller than the data points. The red dotted line indicates the onset of OAE 2; the red bar indicates the Plenus carbon-isotope excursion; the blue bar indicates the PCE *sensu stricto*.

### 3.3. Chromium and cerium concentrations

Chromium and REE concentrations were determined in 35 samples, with chromium concentrations ranging from 0.32–5.48 ppm, with the highest values found in Beds 6–8 of the Plenus Marls (Figure 2). Chromium concentrations peak during the uppermost Plenus interval, reflecting the pattern observed in  $\delta^{18}\text{O}$ . However, the response of Cr lags slightly behind the peaks in  $\delta^{18}\text{O}$ . Previous studies on the Plenus Marls at Eastbourne, Sussex have also identified pulses of Cr enrichment during the Plenus interval (Orth et al., 1993; Pearce et al., 2009; Jenkyns et al., 2017).

REE patterns yielded Ce/Ce\* data with Ce anomalies between 0.5–0.85. The Ce/Ce\* anomalies generally decrease up-section, mirroring the generally increasing pattern of  $\delta^{13}\text{C}$ . While Cerium anomalies are lower during the Plenus interval than prior to the event, there are no observable excursions superimposed onto the decreasing trend (cf. Lu et al., 2010).

#### 4 Discussion of Plenus Cold Event records

Because the Plenus event was first identified in the Chalk of southern England, these exposures will be considered as comprising a composite type-section (Figure 1), using the  $\delta^{13}\text{C}_{\text{carb}}$  record of Tsikos et al. (2004) from Eastbourne and the  $\delta^{18}\text{O}$  record of Lamolda et al. (1994) from Dover, which also yielded the boreal fauna identified by Gale and Christensen (1996). All other records will be correlated to and compared with this composite record. The negative  $\delta^{13}\text{C}$  excursion between peaks ‘a’ and ‘b’ is henceforth referred to as the Plenus carbon-isotope excursion (P-CIE), and the interval of cooling during the ‘second build-up’ will be called the Plenus Cold Event, *sensu stricto* (after Gale and Christensen, 1996). Using this definition, and based on the age model of Kuhnt et al. (2017), the P-CIE lasted ~65 kyr, while the main phase of the cooling (as seen at Eastbourne) lasted ~40 kyr.

##### 4.1 Evidence for change in the carbon cycle

Across the globe, negative carbon-isotope excursions recording the P-CIE are registered in bulk carbonate, bulk marine and terrestrial organic-matter, and compound-specific materials (Figure 3). Notably, the Plenus CIE shows remarkable consistency in its timing and expression across the world in terms of its relationship to, and position in, the overarching positive excursion characteristic of the Cenomanian–Turonian interval. However, care must be taken when interpreting these records in terms of global changes in carbon cycling as local processes

may overprint any global signal. For example, short-term local variations in  $\delta^{13}\text{C}$  may reflect a direct response to transgression–regression cycles, which affect the area of shelf and marginal seas as major sinks for organic matter, or changes in oceanic  $^{12}\text{C}$  storage in response to changing ocean circulation (Jenkyns et al., 1994; Voigt, 2000). Changes in local upwelling may also affect the  $\delta^{13}\text{C}$  record, with waters coming from oxygen-minimum zones having lower seawater  $\delta^{13}\text{C}$  than near-surface dissolved inorganic carbon (Berger and Vincent, 1986). As such, local oceanographic feedbacks may have produced carbon-isotope excursions partially decoupled from the isotopic composition of the global ocean–atmosphere carbon reservoir.



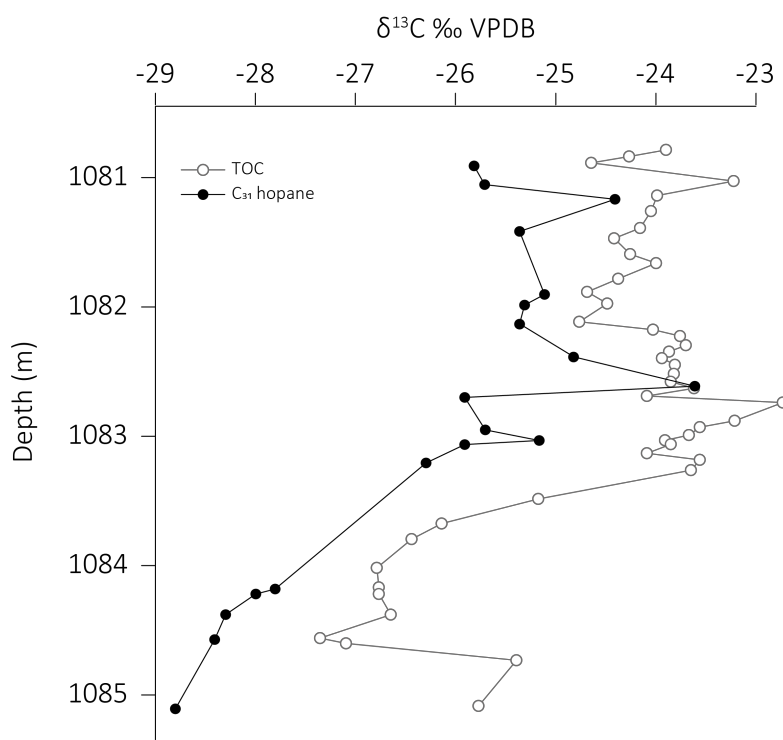
**Figure 3.** Global distribution of known records demonstrating the Plenus CIE (a negative  $\delta^{13}\text{C}$  excursion between points ‘a’ and ‘b’ in Figure 1) or an excursion in  $\text{CO}_2$  across the Plenus interval, as indicated by  $\Delta^{13}\text{C}$ , compound-specific  $\delta^{13}\text{C}$ , or leaf stomata. **1** Pratt’s Landing (van Helmond et al., 2016); Vermillion River, Well 10-35-45-2WA (Prokoph et al., 2013). **2** Cuba, KS (Bowman & Bralower 2015); Pueblo (Barclay et al., 2010; Bowman & Bralower, 2005; Caron et al., 2006; Keller et al., 2008; Pratt et al., 1985; Sageman et al., 2006); USGS Portland-1

core (Eldrett et al., 2017); Aristocrat Angus core (Joo and Sageman, 2014); Hot Springs, CO  
(Desmares et al., 2007); SH#1 core (Jones et al., 2019); generalized Western Interior Seaway  
(Orth et al., 1993). **3** Great Valley Sequence, CA (Du Vivier et al., 2015). **4** Innes-1 core, Iona-1  
core, Well X core (Eldrett et al., 2017). **5** Axaxacoalco, Barranca el Tigre, Barranco el Canon  
(Elrick et al., 2009). **6** Laurichocha, Piedra Parada, Uchucchacua (Navarro-Ramirez et al., 2016,  
2017). **7** Bass River, NJ (Bowman and Bralower, 2005; van Helmond et al., 2013). **8** ODP Site  
1258 (Erbacher et al., 2005); ODP Site 1260 (Eldrett et al., 2017; Erbacher et al., 2005; Forster et  
al., 2007; van Bentum et al., 2012); ODP Site 1261 (Eldrett et al., 2017; Erbacher et al., 2005). **9**  
DSDP Site 367 (Dickson et al., 2016; Forster et al., 2007; Kuypers et al., 1999; Sinninghe  
Damsté et al., 2008). **10** Tarfaya (Keller et al., 2008; Kolonic et al., 2005; Kuhnt et al., 2017;  
Kuypers et al., 2002; Tsikos et al., 2004); Mpl, S57, S75 (Kolonic et al., 2005); S13 (Kuypers et  
al., 1999; Kolonic et al., 2005). **11** ODP Site 1276 (Sinninghe Damsté et al., 2008; van Helmond  
et al., 2014). **12** Arobes, Ganuza, Menoyo (Kaiho et al., 2014); Manilvala (Mort et al., 2007);  
Puentedey (Barroso-Barcenilla et al., 2011). **13** Dover (this study; Jeans et al., 1991; Lamolda et  
al., 1994); Eastbourne (Jenkyns et al., 1994; Paul et al., 1999; Tsikos et al., 2004; Gale et al.,  
2005; Pearce et al., 2009; Zheng et al., 2013); Culver Cliff (Jarvis et al., 2001). **14** Gröbern  
(Voigt et al., 2006); Halle (Voigt et al., 2007); Wunstorf (Voigt et al., 2008; Du Vivier et al.,  
2014); Roter Sattel (Charbonnier et al., 2018). **15** Lambruisse (Takashima et al., 2009); Pont  
d’Issole (Grosheny et al., 2006; Jarvis et al., 2011); les Lattes, Le Bourgeut (Grosheny et al.,  
2017); Cassis (Heimhofer et al., 2018); Clot Chevalier (Gale et al., 2019). **16** Pecínov, Czech  
Republic (Košťák et al., 2017). **17** Bottaccione (Kuroda et al., 2007); Furlo (Mort et al., 2007);  
Gubbio (Jenkyns et al., 1994; Tsikos et al., 2004); Raia del Pedale (Owens et al., 2013); Monte  
Coccovello, Monte Varchera (Parente et al., 2008). **18** Crimea (Fisher et al., 2005). **19** Jerissa

(Zaghib-Turki & Soua 2013); Oued Mellegue (Nederbragt & Fiorentino 1999); Wadi Bahoul (Caron et al., 2006). **20** Wadi Feiran (El-Sabbagh et al., 2011). **21** Ghawr Al Mazar (Wendler et al., 2016); Wadi Karak (Farouk et al., 2017). **22** Aimaki, Khadzalmakhi, Levashi (Gavrilov et al., 2013). **23** Taherabad (Kalanat et al., 2018). **24** Tappu (Nemoto & Hasegawa 2011); Yezo (Du Vivier et al., 2015). **25** ODP Site 530 (Forster et al., 2008). **26** Gongzha (Bomou et al., 2013); Tingri (Li et al., 2006). **27** Sawpit Gully, Mangaotane B (Hasegawa et al., 2013; Gangl et al., 2019); Mangaotane A (Hasegawa et al., 2013).

The carbon-isotope signature of bulk organic matter is especially susceptible to modification by shifts in its composition due to changes in source, preservation, and diagenetic alteration (e.g. Voigt et al., 2006). In many studies, diagenesis has been noted as potentially producing false excursions that make it difficult to determine whether the  $\delta^{13}\text{C}_{\text{org}}$  records reflect paleoenvironmental change or simply local overprinting (Voigt, 2000; Voigt et al., 2006; Jarvis et al., 2006). Changing the ratio of terrestrial to marine organic matter, by either increased input or preferential preservation, will shift the  $\delta^{13}\text{C}$  of the bulk material, potentially giving a false excursion unrelated to global or local carbon cycling. In several instances, bulk-organic and compound-specific  $\delta^{13}\text{C}$  records from a single section show differences between these archives in the structure of the excursion through the OAE 2 interval (e.g. ODP Site 1276, Cape Verde Basin, Sinninghe Damsté et al., 2010; Figure 4), possibly owing to differences in local carbon-cycle processes, as well as changes in the relative abundance of different organic components (Tsikos et al., 2004; Kolonic et al., 2005; Sinninghe Damsté et al., 2010; Gale et al., 2019). Furthermore, differences in the pattern of the  $\delta^{13}\text{C}_{\text{carb}}$  and  $\delta^{13}\text{C}_{\text{org}}$  curves can also be seen within a single section, such as at Tarfaya (Tsikos et al., 2004; Kuhnt et al., 2017), which may indicate

variable fractionation between organic and inorganic carbon, local changes in carbon cycling, and/or possibly diagenetic overprints on the carbonate and/or organic fractions (Jarvis et al., 2006). However, allowing for minor differences due to the aforementioned factors,  $\delta^{13}\text{C}$  curves shows a generally globally consistent evolution across the OAE and Plenus interval at most localities.



**Figure 4.** Comparison of  $\delta^{13}\text{C}_{\text{org}}$  and  $\delta^{13}\text{C}_{\text{hopane}}$  records from ODP Site 1276, Cape Verde Basin (adapted from Sinninghe Damsté et al., 2010) demonstrating a stratigraphic offset in the position of the negative excursion seen in  $\delta^{13}\text{C}_{\text{org}}$  at ~1083.1 mbsf and in  $\delta^{13}\text{C}_{\text{hopane}}$  at ~1082.8 mbsf.

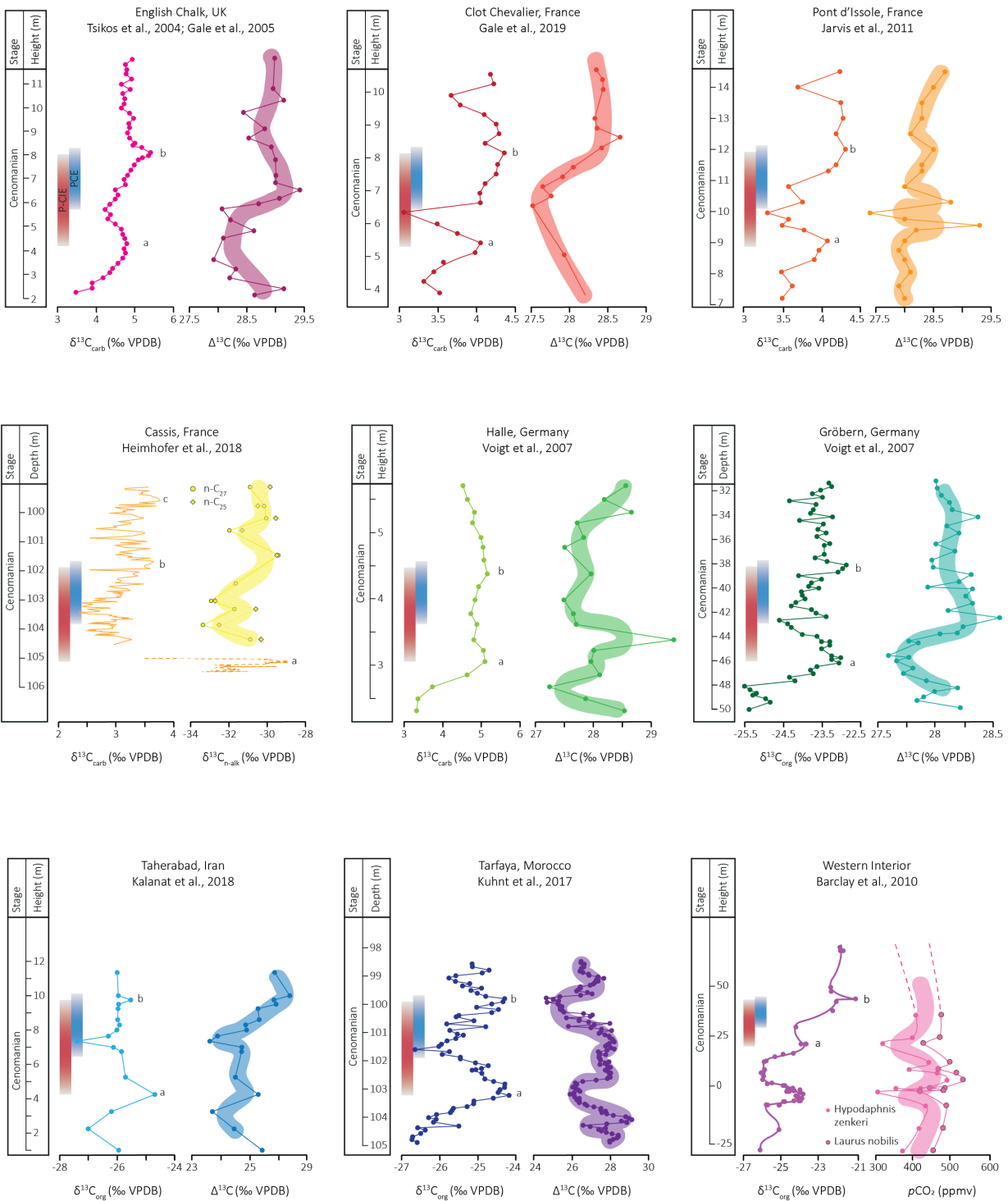
#### 4.1.1. Evidence for change in CO<sub>2</sub>

Reconstructions of atmospheric CO<sub>2</sub> across OAE 2 are few in number (Figure 5) and, in some cases, open to interpretation. A reconstruction of  $p\text{CO}_2$ , based upon values of the stomatal index of fossil leaves from the margins of the Western Interior Seaway, indicates two increases in  $p\text{CO}_2$  values during the early stages of OAE 2, coincident with negative  $\delta^{13}\text{C}_{\text{org}}$  excursions (Barclay et al., 2010). These authors do not specify which event they think correlates with the PCE, but do interpret the decreased stomatal index values as reflecting a global increase in atmospheric  $p\text{CO}_2$  in response to carbon burial. Using integrated bio- and chemostratigraphy, we interpret the P-CIE as the negative  $\delta^{13}\text{C}$  excursion between 25 and 50 m height (Figure 5, cf. Laurin et al., 2019), consistent with the interpretation of Jarvis et al., (2011). While the stomatal data are very sparse across this interval, atmospheric CO<sub>2</sub> appears to rise from point ‘a’ (Figure 5). Regardless of which negative excursion is interpreted to be the P-CIE, a fall in  $\delta^{13}\text{C}$  correlates with a rise in  $p\text{CO}_2$ . Leaf-wax  $\delta^{13}\text{C}$  records from the Cenomanian–Turonian organic-rich sediments from the equatorial Atlantic (Kuypers et al., 1999; Sinninghe Damsté et al., 2010) and France (Heimhofer et al., 2018) suggest a rise in CO<sub>2</sub> from point ‘a’ to the trough of the P-CIE and then a fall to point ‘b’ (Figure 5). Given the similarity in CO<sub>2</sub> trends indicated by these two independent proxies for atmospheric CO<sub>2</sub>, we suggest that the rise in  $p\text{CO}_2$  from point ‘a’ and fall across point ‘b’ likely reflect global changes in the atmosphere.

$\Delta^{13}\text{C}$  (the offset between  $\delta^{13}\text{C}_{\text{carb}}$  and  $\delta^{13}\text{C}_{\text{org}}$  in marine sediments) reflects the degree of carbon fractionation during photosynthesis, which is  $p\text{CO}_2$ -dependent (Farquhar et al., 1989; Freeman & Hayes 1992).  $\Delta^{13}\text{C}$  records changes in dissolved seawater CO<sub>2</sub> concentration, which is assumed to be in equilibrium with atmospheric CO<sub>2</sub>, and thus can be used as a  $p\text{CO}_2$  proxy.  $\Delta^{13}\text{C}$  marine records from the UK, France, Germany, and Morocco show a similar trend to the



360 terrestrial records from the Western Interior Seaway: namely, a rise then fall in CO<sub>2</sub> over the P-  
361 CIE interval (Gale et al., 2005; Voigt et al., 2006, 2007; Jarvis et al., 2011). Two  $\Delta^{13}\text{C}$  records  
362 from France (Gale et al., 2019) and Iran (Kalanat et al., 2018) show different trends: both  
363 indicate an increase in  $p\text{CO}_2$  over the P-CIE, though both show poorly resolved Plenus CIEs  
364 owing to condensation, diagenesis, or poorly resolved stratigraphy.



**Figure 5.** Records of CO<sub>2</sub> change across the Plenus interval. The gray boxes indicate the OAE 2 interval; the red boxes indicate the P-CIE; the blue boxes indicate the PCE *sensu stricto*; points ‘a’ to ‘c’ of the OAE are labelled. Coloured bands illustrate visual approximations of trends.

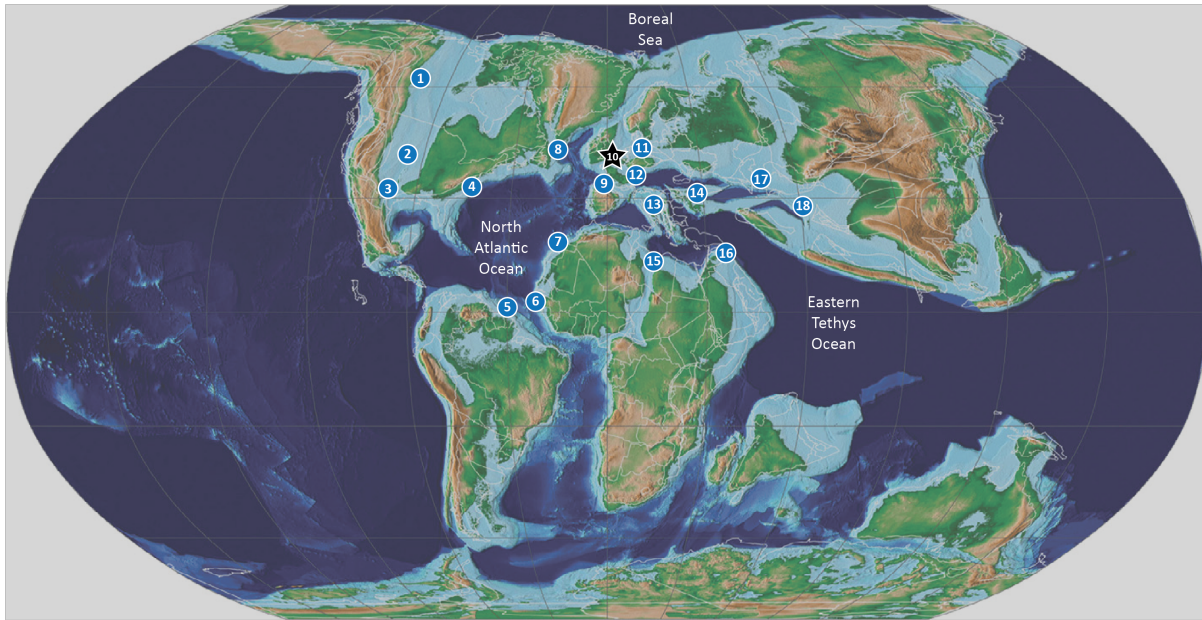
Despite their general agreement with the terrestrial proxies for  $p\text{CO}_2$ ,  $\Delta^{13}\text{C}$  records must be treated with some caution when interpreted in the context of atmospheric CO<sub>2</sub> changes. Changes in oceanography may have generated local variations in ocean CO<sub>2</sub> fluxes and concentrations. For example, the incursion of a cold, oxygenated water-mass across a region would have led to the remineralisation of buried organic-matter, causing a localised increase in [CO<sub>2</sub>] in bottom waters and potentially, particularly in areas of upwelling, to CO<sub>2</sub> outgassing to the atmosphere. As the total organic-carbon (TOC) content of strata varied regionally, the degree of remineralization would have varied between sites, producing different CO<sub>2</sub> concentrations in different locations. Furthermore, as CO<sub>2</sub> solubility is dependent on water temperature (e.g. Broecker & Peng 1974), a cold water-mass would contain higher concentrations of dissolved CO<sub>2</sub> compared with warmer waters, and this alone would have affected the local pH without involving any atmospheric processes. Euxinic conditions may also affect local CO<sub>2</sub> concentrations, as the degradation of organic-matter allows phosphate to be released back to bottom-waters, driving increased productivity and organic-matter deposition (Mort et al., 2007; Jarvis et al., 2011). These local processes could potentially mask any signal of atmospheric  $p\text{CO}_2$  change and, if not recognized, could lead to erroneous interpretations of the drivers of the PCE.

## 4.2 Evidence for changing temperature

The Plenus Cold Event was first recognized based on the southerly migration of boreal fauna coincident with two positive  $\delta^{18}\text{O}$  excursions in the Chalk of Dover, UK (Jefferies et al., 1962; Gale & Christensen 1996). In the Dover Chalk records, cooling is observed in Beds 2 and 4–8 of the Plenus Marls (Figures 1 and 2), supported by numerous other records of faunal assemblages and  $\delta^{18}\text{O}$  from southeast England, with some variation in the timing of the onset of cooling (this study; Jefferies, 1962, 1963; Jeans et al., 1991; Lamolda et al., 1994; Paul et al., 1999; Tsikos et al., 2004; Voigt et al., 2004, 2006; Gale et al., 2005). The main phase of cooling in southeast England, as exemplified by the carbon-isotope record, extends from the trough of the P-CIE to point ‘b’.

The early stages of OAE 2 have been studied extensively across the Northern Hemisphere, with multiple quantitative and qualitative records indicating brief cooling around the P-CIE interval (Figure 6).  $\delta^{18}\text{O}$  (Kuhnt et al., 2017; Kalanat et al., 2018),  $\text{TEX}_{86}$  (Forster et al., 2007; Sinninghe Damsté et al., 2010), faunal assemblages (van Helmond et al., 2013, 2016; Eldrett et al., 2017), and foraminiferal coiling direction (Desmares et al., 2016) show clear evidence for cooling across the Tethyan margins, North Atlantic, and Western Interior Seaway. In France and Germany, incursions of boreal fauna and dinocysts also indicate cooling, as supported by  $\delta^{18}\text{O}$  and  $\text{TEX}_{86}$  records (Figure 7; Takashima et al., 2009; Voigt et al., 2006, 2007, 2008; van Helmond et al., 2015). However, some bulk  $\delta^{18}\text{O}$  records from hemipelagic clay-rich carbonates (e.g. Pont d’Issole, Vocontian Basin, France) show no clear excursion across the PCE interval (Voigt et al., 2006; Jarvis et al., 2011), even though nearby sections, a few tens of kilometres away, show distinct positive excursions of 1–1.5‰ locally alongside qualitative measures of

cooling, such as changes in the direction of foraminiferal coiling (Grosheny et al., 2017; Gale et al., 2019).

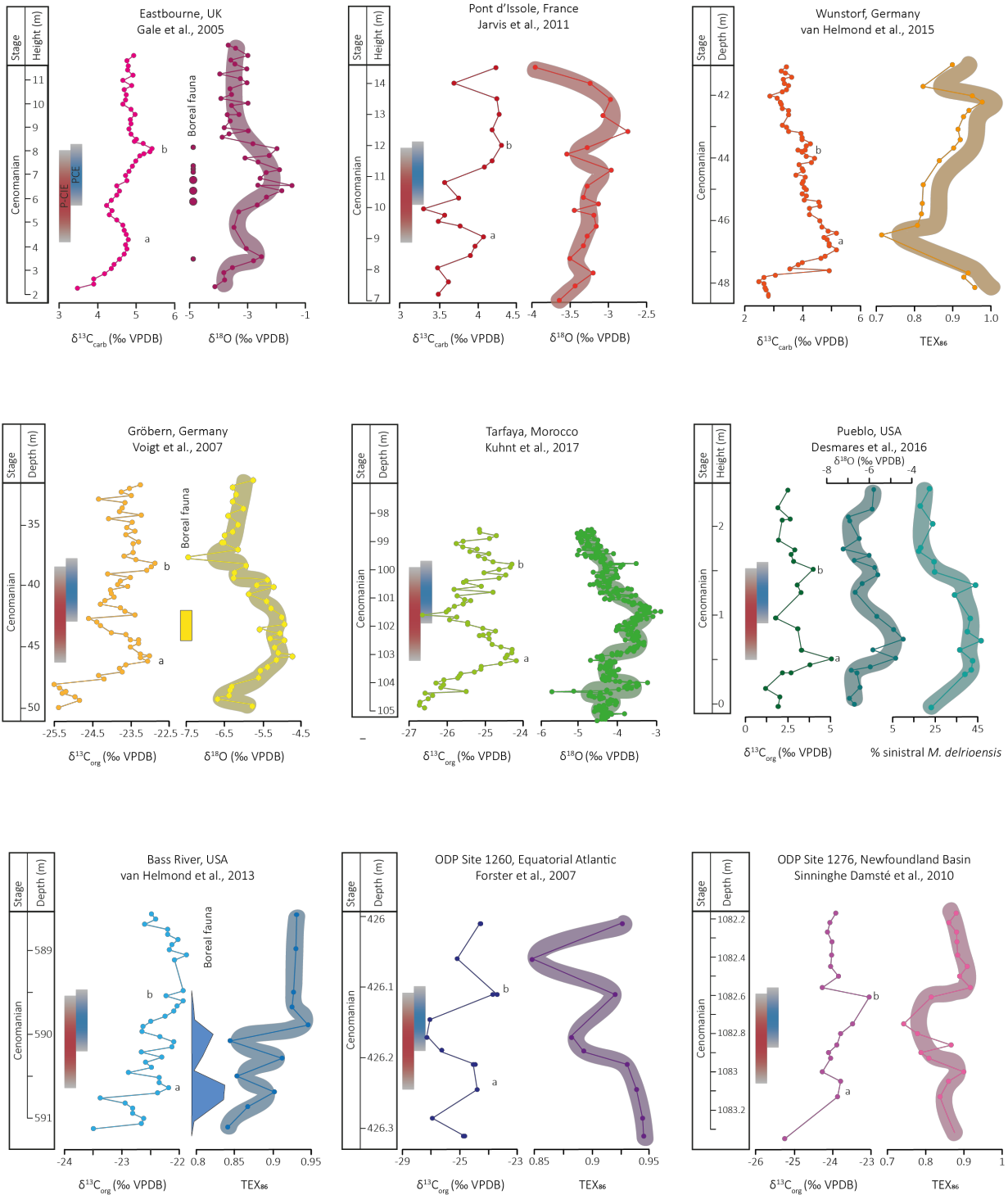


**Figure 6.** Global distribution of known records demonstrating a change in temperature across the PCE interval, based on records of  $\text{TEX}_{86}$ ,  $\delta^{18}\text{O}$ , faunal assemblages, and foraminiferal coiling. **1** Pratt's Landing (van Helmond et al., 2016). **2** Hot Springs, SD (Desmares et al., 2016); Pueblo (Caron et al., 2006; Desmares et al., 2016); USGS Portland-1 Core (Eldrett et al., 2017). **3** Iona-1 core, Innes-1 core, Well X core (Eldrett et al., 2017). **4** Bass River, NJ (van Helmond et al., 2013). **5** ODP Site 1260 (Forster et al., 2007; Eldrett et al., 2017). **6** DSDP Site 367 (Forster et al., 2007). **7** Tarfaya (Tsikos et al., 2004; Kuhnt et al., 2017). **8** ODP Site 1276 (Sinninghe Damsté et al., 2008). **9** Arobes, Ganuza, Menoyo (Kaiho et al., 2014); Puentedey (Barroso-Barcenilla et al., 2011). **10** Dover (this study; Jefferies 1962; Jeans et al., 1991; Lamolda et al., 1994); Eastbourne (Jenkyns et al., 1994; Paul et al., 1999; Tsikos et al., 2004; Voigt et al., 2004, 2006; Pearce et al., 2009; Zheng et al., 2013). **11** Gröbern (Voigt et al., 2006); Halle (Voigt et al., 2007); Wunstorf (van Helmond et al., 2015). **12** Cassis (Heimhofer et al., 2018); Clot Chevalier

(Gale et al., 2019); Lambruisse (Takashima et al., 2009); les Lettes (Gale & Christensen 1996); Pont d'Issole (Jarvis et al., 2011). **13** Gubbio (Jenkyns et al., 1994). **14** Crimea (Fisher et al., 2005). **15** Oued Mellegue (Nederbragt & Fiorentino 1999); Wadi Bahoul (Caron et al., 2006). **16** Wadi Karak (Farouk et al., 2017). **17** Amaki, Khadzalmakhi, Levashi (Gavrilov et al., 2013). **18** Taherabad (Kalanat et al., 2018).

Although cooling appears to be geographically widespread, the precise timing of the falls in local paleotemperature is not consistent globally, or even within a single basin. For example, in Germany, Pueblo and DSDP Site 367, cooling starts well before the P-CIE and reaches its lowest temperature around point 'a', based on TEX<sub>86</sub>,  $\delta^{18}\text{O}$ , foraminiferal coiling, and faunal assemblages (Figure 7; Voigt et al., 2007; Forster et al., 2007; van Helmond et al., 2015; Desmares et al., 2016). By contrast, in the Chalk records from southern England, and TEX<sub>86</sub> records from DSDP Site 367 (Equatorial Atlantic) and ODP Site 1276 (North Atlantic), the cooling apparently started later and peaked around point 'b' (Lamolda et al., 1994; Gale and Christensen, 1996; Forster et al., 2007; Sinninghe Damsté et al., 2010). Other sites, such as Tarfaya and ODP Site 1260 suggest a more complex pattern of cooling, with multiple excursions in the TEX<sub>86</sub> and  $\delta^{18}\text{O}$  records (Forster et al., 2007; Kuhnt et al., 2017). However, Tarfaya is recognized as a paleo-upwelling area, which would have complicated the SST response (e.g. Einsele and Wiedmann, 1982; Kolonic et al., 2005). Although local diagenesis may have affected some of the SST records, in particular those deriving from oxygen isotopes, the existence of consistent differences in the relative timing between carbon-isotope events and local paleotemperature minima (based on both geochemical and paleontological proxies) suggests that the cooling of water-masses was diachronous.

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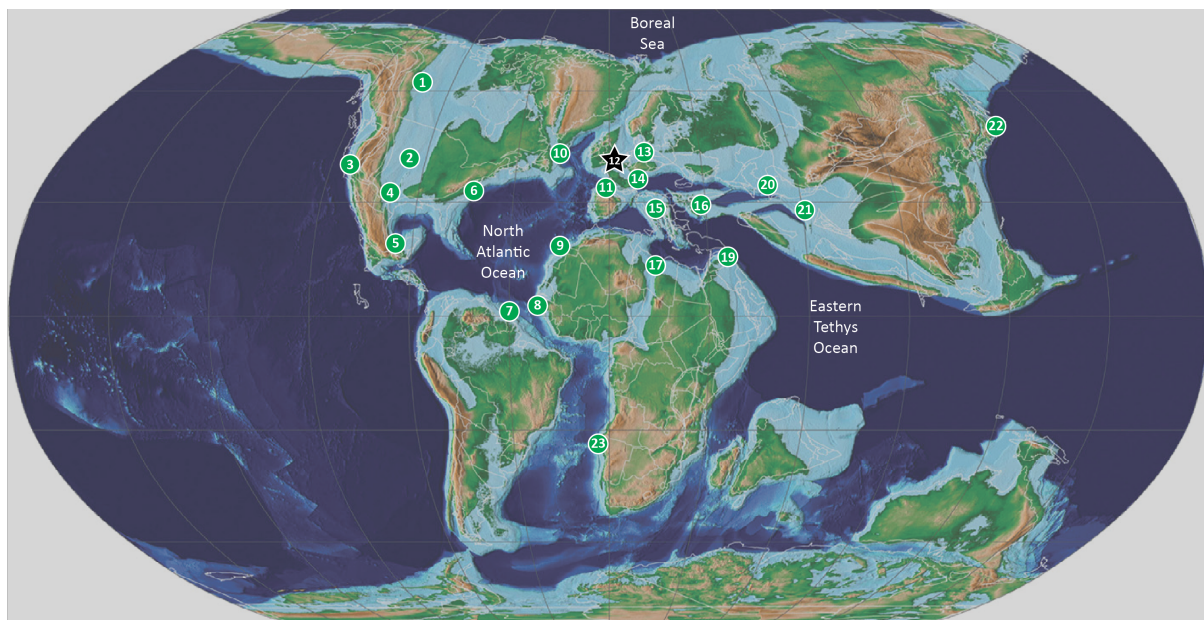


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**Figure 7.** Records of SSTs during the Plenus interval. The gray boxes indicate the OAE 2 interval; the red boxes indicate the P-CIE; the blue boxes indicate the PCE *sensu stricto*; points ‘a’ to ‘c’ of the OAE are labelled. Dover stratigraphy from Lamolda et al., 1994; Wunstorff stratigraphy from Voigt et al., 2008. Coloured bands illustrate visual approximations of trends.

#### 4.2 Evidence for changing water-mass character

Geochemical, lithological, and faunal records across OAE 2 demonstrate significant and variable changes in water-mass character associated with the event, variously attributed to changes in redox, circulation, and/or volcanic activity (Figure 8; e.g. Eicher and Worstell, 1970; Orth et al., 1993; MacLeod et al., 2008; Martin et al., 2012; Thomas & Tilghman 2014). However, few records are of sufficiently high resolution to both identify the Plenus interval and any oceanographic changes associated therewith and determine the precise cause of these changes.





**Figure 8.** Global distribution of known records demonstrating a change in water-mass character across the Plenus interval, as indicated by elemental, isotopic, lithological, or faunal changes in the sedimentary record. **1** Vermillion River (Prokoph et al., 2013). **2** Angus Aristocrat core (Zhou et al., 2015); Cuba, KS (Bowman & Bralower 2015; Elderbak et al., 2014); Hot Springs, SD (Desmares et al., 2016); USGS Portland-1 core (Du Vivier et al., 2014; Holmden et al., 2016; Eldrett et al., 2017); generalized Western Interior Seaway (Orth et al., 1993); Pueblo (Bowman & Bralower, 2005; Caron et al., 2006; Keller et al., 2008; Elderbak et al., 2014). **3** Great Valley Sequence, CA (Du Vivier et al., 2015). **4** Innes-1 core, Iona-1 core, Well X core (Eldrett et al., 2017). **5** Barranco el Canon (Elrick et al., 2009; Sweere et al., 2018). **6** Bass River, NJ (Bowman and Bralower, 2005). **7** ODP Site 1258 (Erbacher et al., 2005; Friedrich et al., 2006; Ostrander et al., 2017; Zhou et al., 2015); ODP Site 1260 (Erbacher et al., 2005; Friedrich et al., 2006; Forster et al., 2007; Turgeon and Creaser, 2008; Du Vivier et al., 2014; Eldrett et al., 2017); ODP Site 1261 (Erbacher et al., 2005; Friedrich et al., 2006). **8** DSDP Site 367 (Kuypers et al., 1999; Forster et al., 2007, 2008; Sinninghe Damsté et al., 2008; Du Vivier et al., 2014; Dickson et al., 2016). **9** Tarfaya (Kuypers et al., 2002; Tsikos et al., 2004; Keller et al., 2008; Dickson et al., 2016; Kuhnt et al., 2017); Mpl, S13, S57, S75 (Kolonis et al., 2005). **10** ODP Site 1276 (Sinninghe Damsté et al., 2008; van Helmond et al., 2014). **11** Puentevedey (Barroso-Barcenilla et al., 2011); Arobes (Kaiho et al., 2014); Ganuza (Peryt and Lamolda, 1995; Kaiho et al., 2014); Manivala (Mort et al., 2007); Menoyo (Peryt and Lamolda, 1995; Kaiho et al., 2014). **12** Dover (this study; Jeans et al., 1991); Eastbourne (Orth et al., 1993; Paul et al., 1999; Pearce et al., 2009; Lu et al., 2010; Owens et al., 2013; Zheng et al., 2013; Zhou et al., 2015; Clarkson et al., 2018; Sweere et al., 2018). **13** Wunstorf (van Helmond et al., 2015); Halle (Voigt et al., 2007); Roter Sattel (Charbonnier et al., 2018); Wunstorf (Du Vivier et al., 2014; van Helmond et al.,

2015). **14** Clot Chevalier (Gale et al., 2019); Lambruisse (Takashima et al., 2009); Le Bourgeut  
 (Grosheny et al., 2017); Pont d'Issole (Grosheny et al., 2006; Jarvis et al., 2011; Danzelle et al.,  
 2018); Vocontian Basin (Du Vivier et al., 2014). **15** Bottaccione (Kuroda et al., 2007); Furlo  
 (Mort et al., 2007); Gubbio (Tsikos et al., 2004); Raia del Pedale (Owens et al., 2013; Zhou et  
 al., 2015; Clarkson et al., 2018; Sweere et al., 2018). **16** Crimea (Fisher et al., 2005). **17** Oued  
 Mellegue (Nederbragt & Fiorentino 1999); Wadi Bahoul (Caron et al., 2006). **18** Wadi Feiran  
 (El-Sabbagh et al., 2011). **19** Wadi Karak (Farouk et al., 2018). **20** Aimaki, Khadzalmakhi,  
 Levashi (Gavrilov et al., 2013). **21** Gharesu (Kalanat et al., 2016); Taherabad (Kalanat et al.,  
 2016, 2017). **22** Tappu (Nemoto & Hasegawa 2011); Yezo Group (Du Vivier et al., 2015). **23**  
 DSDP Site 530 (Forster et al., 2008; Du Vivier et al., 2014). **24** Gongzha (Bomou et al., 2013).

Chromium is a redox-sensitive metal that may also be derived from basalt–seawater  
 interactions, and as such is a useful tool for tracking changes in seawater chemistry (e.g.  
 Bonnard et al., 2013; Holmden et al., 2016; Remmelzwaal et al., 2019). At Dover in SW  
 England, carbonate-fraction Cr concentrations show a ~5-fold increase over the uppermost marls  
 (this study; Figure 2). Similar spikes in geochemical species (such as Cr, Mo, U, Mn) have been  
 recorded at sites in the Chalk Sea and/or along the Tethyan margins (e.g. Orth et al., 1993; Jarvis  
 et al., 2001; Kolonic et al., 2005; Pearce et al., 2009; Jenkyns et al., 2017; Charbonnier et al.,  
 2018; Clarkson et al., 2018; Danzelle et al., 2018; Sweere et al., 2018; Gale et al., 2019), North  
 Atlantic (van Helmond et al., 2014; Dickson et al., 2016; Eldrett et al., 2017) and the Western  
 Interior Seaway (Orth et al., 1993; Holmden et al., 2016; Eldrett et al., 2017). These excursions  
 have been attributed to a period of increased bottom-water oxygenation during which the  
 remineralisation of organic-matter either released trace metals into the water column and/or

508 removed anoxic/euxinic sinks for hydrothermally enriched bottom waters (Jenkyns et al., 2017).  
509 However, some sites show excursions in certain geochemical species but not others (e.g. Owens  
510 et al., 2013; Eldrett et al., 2017; Danzelle et al., 2018; Sweere et al., 2018). These differences  
511 may be due to the different reduction potentials of various elements and the local redox  
512 conditions pertaining at any one site. Local redox conditions during the Plenus interval may have  
513 prevented certain elements from being enriched in discrete reduced phases, such as in sulphides,  
514 or substituting in pyrite or adsorbed onto organic matter but not allowed them to be incorporated  
515 in carbonates in more oxidized form even if present in relative abundance in  
516 seawater. Regardless of the cause, these variable expressions of redox change across the Plenus  
517 interval make it difficult to deconvolve global from local drivers of paleoenvironmental change.

518 Neodymium-isotope ratios, expressed as  $\epsilon_{\text{Nd}}$ , are a powerful tool for reconstructing  
519 changes in past ocean circulation (Frank, 2002; Goldstein and Hemming, 2003). Roughly coeval  
520 with the Cr excursion in the Chalk of SW England, large ( $\sim 1.5$   $\epsilon$  unit) excursions in neodymium  
521 isotopes across the PCE interval suggest changing circulation and/or possible input of  
522 magmatically derived radiogenic Nd (this study; Zheng et al., 2013, 2016). A link has been  
523 drawn between LIPs and oceanic anoxic events, particularly with respect to the Caribbean and  
524 High Arctic Large Igneous Provinces as possible triggers for OAE 2 (e.g. Snow et al., 2005;  
525 Tegner et al., 2011; Zheng et al., 2013). Osmium-isotope records from across the world have  
526 identified periods of volcanism or some form of basalt–seawater interaction around the  
527 Cenomanian–Turonian boundary, indicating likely LIP activity immediately prior to the onset of  
528 OAE 2 (Turgeon and Creaser, 2008; Du Vivier et al., 2014, 2015; Scaife et al., 2017; Schröder-  
529 Adams et al., 2019). Basalt–seawater interactions would not have just affected seawater Nd and

Os, but also other trace metals and isotopes, which further complicates the interpretation of their sedimentary records.

Ce anomalies reflect the oxidation state of seawater through the oxidation of Ce (III) to insoluble and particle-reactive Ce (IV) (De Baar et al., 1988; Zhou et al., 2016; Remmelzwaal et al., 2019). In the Dover record, Ce\* steadily decreases up-section, mirroring the generally increasing pattern of  $\delta^{13}\text{C}$ . These data can be compared with trace-element data from the Eastbourne section (Lu et al., 2010; Jenkyns et al., 2016). Cerium anomalies at Dover are generally lower during the PCE than prior to the event, but there is a significant increase in Ce/Ce\* from 0.7 to 0.83 at the beginning of the OAE event in the Dover section. This rise is consistent with Mn/Ca data for the Eastbourne section, suggestive of an initial move to a less oxic sub-seafloor, whereas the overall decrease in Ce/Ce\*, particularly during the PCE is consistent with I/Ca ratios indicating a move to more oxic surface waters at this time (Lu et al., 2010). Seawater and carbonates in modern marine environments commonly have both Ce and La anomalies and this is best demonstrated by calculating Ce/Ce\* and Pr/Pr\* values, which also co-vary with each other (Webb and Kamber, 2000). Our new carbonates record indicates that the late Cenomanian seawater also has both Ce and La anomalies. While Ce/Ce\* and Pr/Pr\* (not shown) values vary smoothly through the section, they are principally indicative of variable redox conditions, whereas La/Pr ratios still retain information about source input and are much more variable. In this case, the La/Pr ratio is a useful guide to the amount of basaltic input to the seawater because average altered basaltic crust has La/Pr value of 1.65 (Kelley et al, 2003) whereas the upper continental crust has a value of 4.37 (Rudnick and Gao, 2003). Therefore, lower La/Pr ratios are indicative of an increased basaltic input, either from basalt–seawater interaction or re-oxygenation of sea-floor sediment. La/Pr ratios decrease at the beginning of the

OAE level and during the interval of the two cooling events, particularly the main PCE, at which level it is consistent with positive shifts in Nd isotopes.

Re-oxygenation of bottom water has also been invoked as the cause of decreased TOC in Plenus records from the Tethys, North Atlantic, and even Japan (Tsikos et al., 2004; Bowman & Bralower 2005; Forster et al., 2007; Sinninghe Damsté et al., 2010; Jarvis et al., 2011; Nemoto & Hasegawa 2011; van Helmond et al., 2013, 2014; Eldrett et al., 2014, 2017; Dickson et al., 2016; Kunht et al., 2017). However, many sites record no change in the TOC, or in some cases an increase, suggesting locally sustained bottom-water oxygenation or simply changes in productivity (e.g. Kuypers et al., 2002; Tsikos et al., 2004; Kolonic et al., 2005; Mort et al., 2007; Gavrilov et al., 2013; Dickson et al., 2016; Kuhnt et al., 2017).

Faunal records showing an increase in benthic organisms and bioturbation during the Plenus interval suggest increased bottom-water oxygenation at sites across the Chalk Sea of northern Europe (Jarvis et al., 1988; Peryt and Lamolda, 1995; Paul et al., 1999; Takashima et al., 2009), Tethyan margin (Barroso-Barcenilla et al., 2011; Kalanat et al., 2016), North Atlantic (Eldrett et al., 2017), and Western Interior Seaway (Desmares et al., 2007; Elderbak et al., 2014). However, as with the TOC records, some sites show no change in benthic faunal abundance over this interval, or in some cases a decrease, further suggesting locally sustained bottom-water anoxia (e.g. Grosheny et al., 2006, 2017; Friedrich et al., 2006; Keller et al., 2008; El-Sabbagh et al., 2011).

Trace-metal, isotope, TOC, and faunal records all suggest pockets of re-oxygenation, but it remains difficult to link these directly to global changes in the carbon cycle or temperature. Furthermore, different water depths at different sites will have directly influenced bottom-water oxygenation, and may determine whether anoxia could have occurred in the first place.

## **5 Implications for understanding environmental changes during the Plenus Cold Event**

### **5.1 Carbon-cycle perturbation**

The remarkable consistency of the carbon-isotope signature of OAE 2 across the globe allows for chemostratigraphic correlation of the event, albeit with the caveat that variable organic-matter sources can affect bulk  $\delta^{13}\text{C}_{\text{org}}$  and variable diagenesis can affect  $\delta^{13}\text{C}_{\text{carb}}$ , particularly in sediments containing potentially reactive organic matter.

In a comparison of bio- and chemostratigraphy of OAE 2 between Europe and North America, Gale et al. (1993) found a consistent relationship between the two, which these authors took as evidence for effective synchronicity between certain paleontological markers and the carbon-isotope events in Europe and North America (despite some endemism and preservation problems, particularly associated with facies changes). More recent and higher-resolution studies support this contention, namely global parallels in the general patterns of microfossil and macrofossil biostratigraphy and  $\delta^{13}\text{C}$  correlations (Jarvis et al., 2006; Wendler 2013). These records indicate a globally synchronous response of the bio- and chemostratigraphic record to the OAE, and that the characteristic carbon-isotope signature can be reliably used in correlation.

The terrestrially derived  $\text{CO}_2$  records and the majority of marine  $\text{CO}_2$  records show a rise then fall in atmospheric  $\text{CO}_2$  across the P-CIE, suggesting a global carbon-cycle event. As such, we propose that the negative  $\delta^{13}\text{C}$  excursion could—and should—be used as a stratigraphic marker to identify the Plenus interval in local archives. This approach to stratigraphic correlation avoids potential miscorrelation issues caused by possible diachroneity of any cooling observed at different locations, which could have been impacted by the local oceanographic conditions.

The driver of this CO<sub>2</sub> change is more difficult to identify. Initially it was proposed that increased organic-carbon burial during the initial stages of OAE 2 drove a drawdown of atmospheric CO<sub>2</sub> (Arthur et al., 1988; Freeman & Hayes 1992; Jenkyns et al., 1994; Kuypers et al., 1999; Forster et al., 2007; Sinninghe Damsté et al., 2010; Jarvis et al., 2011). Therefore, an increase in bottom-water re-oxygenation during the Plenus interval would have led to a temporary reduction of organic-matter deposition and/or the remineralisation of sedimentary carbon on the sea floor, driving an increase in CO<sub>2</sub>. The Cenomanian–Turonian boundary was also a period of enhanced basalt–seawater interaction owing to the emplacement of at least two large igneous provinces (LIPs): the Caribbean Large Igneous Province (CLIP; Snow et al., 2005) and the High Arctic Large Igneous Province (HALIP; Tegner et al., 2011; Davis et al., 2017; Kingsbury et al., 2018; Schröder-Adams et al., 2019). A cessation of this outgassing may have resulted in an overall decrease in *p*CO<sub>2</sub> (e.g. Turgeon & Creaser, 2008; Du Vivier et al., 2014, 2015; Scaife et al., 2017). Indeed, Kuroda et al. (2007) suggested, based on a coeval shift in Pb isotopes indicative of an increase in hydrothermal input of Pb, that the negative carbon-isotope excursion observed during the Plenus interval reflects an increase in *p*CO<sub>2</sub> due to volcanism, rather than a drop in global burial rates of organic carbon. The changing balance between CO<sub>2</sub> drawdown due to organic-carbon burial versus volcanic and tectonic emissions of this greenhouse gas is difficult to constrain. However, a rise in atmospheric CO<sub>2</sub> would drive an increase in global temperatures—the opposite of what is observed. This apparent mismatch between theory and observation highlights complications in drawing causative links between putative CO<sub>2</sub> levels and the PCE, as it was originally interpreted.

## 5.2 Accompanying climatic phenomena

There is a wealth of data indicating widespread paleoenvironmental change during the early stages of OAE 2 but the question remains as to what drove such phenomena in different parts of the globe. Accounting for problems inherent in bio-, chemo-, and lithostratigraphic correlation, the records show little consistency in the timing of temperature and seawater chemistry (Figures 5 and 7). The onset of these changes apparently appeared much earlier at some sites than others, even locally preceding the negative carbon-isotope excursion, suggesting that oceanic processes may have responded to forcing mechanisms other than just changes in ocean–atmosphere  $p\text{CO}_2$ , such as a change in local circulation, productivity, or basalt–seawater interactions.

### 5.3.1 Changing water-mass character

A change in circulation, bottom-water re-oxygenation, and basalt–seawater interactions have variously been proposed to drive the excursions seen in different proxy records discussed in Section 4.3. However, records of seawater chemistry are difficult to interpret as the proxies may have responded to more than one process, or one process may have driven another. The neodymium-isotopic signal of a water-mass may reflect changes in circulation, but it can also be affected by basalt–seawater interaction introducing radiogenic Nd. Although complicating the interpretation of  $\epsilon_{\text{Nd}}$  records, the geochemical imprint of basalt on seawater may be helpful for tracing the source of a water-mass to volcanically affected areas.

The positive  $\epsilon_{\text{Nd}}$  excursion in the Eastbourne record was interpreted by Zheng et al. (2016) to reflect the input of strongly radiogenic Nd from volcanism through relatively oxygen-poor water, citing the coeval emplacement of the Caribbean Large Igneous Province (Snow et al., 2005) and the High Arctic Large Igneous Province (Tegner et al., 2011; Davis et al., 2017;



Kingsbury et al., 2018). Due to the lack of outcrop, the chemistry and eruption history of these LIPs are poorly constrained, which makes it difficult to pinpoint the source of any volcanically derived radiogenic Nd. For CLIP to have acted as the source of radiogenic Nd would have required transfer of the geochemical bottom-water signal from the Pacific Ocean to southern England across the eastern paleo-Pacific and proto-Atlantic (cf. Trabucho Alexandre et al., 2010). Given that the residence time of neodymium in the ocean today is roughly equal to the mixing time of the ocean (Frank, 2002; Goldstein & Hemming 2003; Thomas 2005), CLIP-derived radiogenic Nd is unlikely to have induced such a large positive shift in  $\epsilon_{\text{Nd}}$  in such a distal location as southern England. Neodymium might have had a longer residence time in relatively deoxygenated seawater because Fe-Mn oxyhydroxides (a sink for Nd) would not have been stable under such conditions (Halliday et al., 1992); however, such conditions would have been less applicable during the apparently more oxygenated conditions (at least in southern England) of the PCE itself. If a water-mass from the vicinity of the HALIP moved south, carrying a radiogenic Nd signature, it could have produced a positive  $\epsilon_{\text{Nd}}$  excursion while simultaneously causing a drop in water temperature, as seen in the Dover record (Figure 2). Furthermore, as  $\text{O}_2$  solubility is dependent on water temperature (e.g. Broecker & Peng 1974), a cold water-mass would have contained higher concentrations of dissolved  $\text{O}_2$  compared with warmer waters and could have induced a redox shift in bottom-waters, as suggested by the trace-metal record at Dover (Figure 2) and Eastbourne (Jenkyns et al., 2017).

Trace-metal and isotopic excursions have been ascribed to two factors: 1) bottom-water re-oxygenation during the PCE, whereby the remineralisation of trace-metal-rich organic matter deposited during the early stages of the OAE released metals into the water column, some of which were subsequently incorporated into nannofossil and foraminiferal carbonate (Jenkyns et

al., 2017); and 2) alternatively, or additionally, the transient loss of the organic-rich sink during re-oxygenation events during the Plenus interval, with ongoing basalt–seawater interaction continuing to liberate volcanically derived trace metals, allowed their build-up in ocean waters (Orth et al., 1993; Pearce et al., 2009; Holmden et al., 2016; Jenkyns et al., 2017).

Decreased TOC across the Plenus interval has also been suggested to indicate a redox shift (e.g. Tsikos et al., 2004; Jarvis et al., 2011; Eldrett et al., 2014, 2017), although organic-matter content may be affected by changes in preservation, productivity, or dilution. Increased oxygenation of bottom-waters would inhibit the deposition of organic matter, though this assumes a simple coupling between anoxia and organic-matter deposition in the first place, which is manifestly a gross simplification (e.g. Demaison and Moore, 1980; Pedersen and Calvert, 1990). Deposition of the characteristic black shales of OAE 2 was not a global phenomenon, but rather limited to environments that favourably supported organic-matter burial, particularly the Atlantic and Tethyan regions and the equatorial Pacific (Schlanger et al., 1987; Takashimi et al., 2009). Furthermore, local to regional variations in productivity, preservation, sedimentation rate, and seawater chemistry led to differences in the timing of local maxima in organic-carbon burial rates. Particularly in former upwelling areas, such as the western sides of continents or the paleo-Equator, increases in organic productivity, initially unrelated to bottom- or mid-water redox, may have driven an increase in organic-matter deposition. An increased supply of biologically significant metals or minerals may also have resulted directly from basalt–seawater interactions, and/or increased terrestrial weathering, and consequent accelerated fluvial nutrient input to the oceans, which may in turn have driven an expansion of organic productivity (Jenkyns, 2010). Local changes in these processes—whether related or unrelated to global CO<sub>2</sub> and temperature—may have driven either an increase or decrease in organic-matter deposition

that might be misconstrued as a redox shift. These factors may also explain the records of increased TOC across the Plenus interval in Spain (Mort et al., 2007) and Morocco (Kuhnt et al., 2017). Given the enhanced hydrological cycle, proposed to have driven an increase in silicate weathering during the OAE (Blättler et al., 2011; Pogge van Strandmann et al., 2013), changes in terrestrial weathering and sedimentary dilution may also have affected the TOC without changing productivity or preservation.

### 5.3.1 Cooling

Cooling events are observed across the Northern Hemisphere during the Plenus interval, for which a range of mechanisms has been proposed:

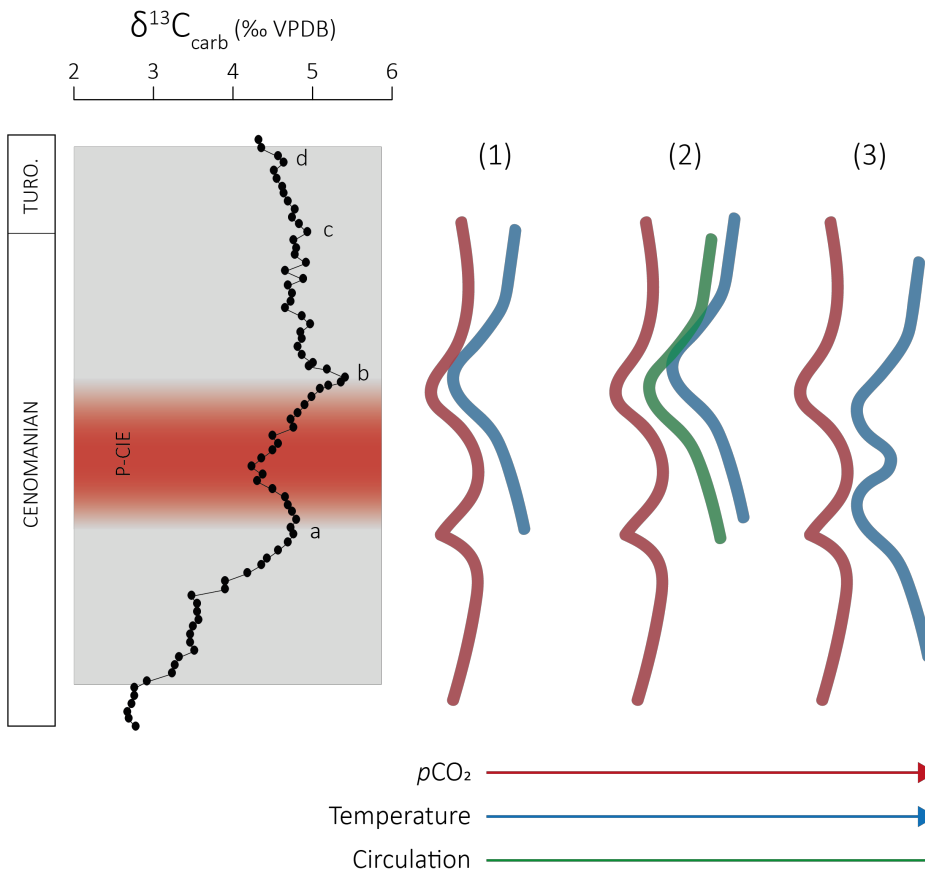
(1) A causal link has been suggested between SSTs and the carbon cycle during OAE 2: at its simplest, the widespread deposition of organic matter during OAE 2 is credited with leading to CO<sub>2</sub> drawdown and, in turn, transient cooling (Arthur et al., 1988; Freeman & Hayes 1992; Jenkyns et al., 1994; Kuypers et al., 1999; Forster et al., 2007; Sinninghe Damsté et al., 2010; Jarvis et al., 2011). However, if these temperature records (TEX<sub>86</sub>,  $\delta^{18}\text{O}$ , fauna) were solely recording the SST response to global atmospheric cooling, they would be expected to show a degree of synchronicity and expression: cooling occurring *during and after* the CO<sub>2</sub> decrease, during the later phase of the P-CIE close to point ‘b’ (e.g. scenario (1) in Figure 9; Eastbourne and ODP Site 1276 in Figure 7). While a global decrease in temperatures would have been a necessary response to falling atmospheric CO<sub>2</sub> levels, the SST records—if accepted at face value—show significant variability in the timing of the cooling relative to the P-CIE. The TEX<sub>86</sub>,  $\delta^{18}\text{O}$ , and faunal records that show cooling preceding the CO<sub>2</sub> decrease, in the early phase of the P-CIE close to point ‘a’ (e.g. Wunstorf, Gröbern, Bass River, Pueblo; Figure 7), which implies either an indirect response of local SSTs to CO<sub>2</sub> change, or simply the effect of

local oceanographic conditions independent of global change. Furthermore, it is difficult to directly link the cooling seen at point 'b' to global processes, when the drop in temperature may have been due to a circulation change bringing cooler water to a locality (as seen by the simultaneous cooling and Nd excursion in SE England) (Figures 2 and 9).

(2) Ocean circulation is thought to have been a critical component of the climate system during the Plenus interval, wherein CO<sub>2</sub> drawdown led to global cooling and increased latitudinal temperature gradients, which in turn drove a change in circulation (Zheng et al., 2013; van Helmond et al., 2014; Eldrett et al., 2017). However, there are two problems with this hypothesis. Firstly, as in (1), this model does not account for cooling preceding the CO<sub>2</sub> decrease. Secondly, if global cooling drove the circulation change, one would expect one phase of cooling after the CO<sub>2</sub> change then another after the circulation change, but none of the records show this. As such, this model cannot account for cooling in the early phase of the P-CIE, close to point 'a', which indicates that CO<sub>2</sub>-driven circulation change was not a direct driver of the cooling at all sites.

(3) Alternatively, circulation might have been altered due to factors unrelated to global temperatures and latitudinal gradients, perhaps owing to changes in upwelling (e.g. Einsele and Wiedmann 1982; Kolonic et al., 2005), deepening and shallowing of local sea levels affecting upper-ocean circulation patterns (e.g. Hancock, 1993; Voigt and Wiese, 2000; Voigt et al., 2006), or LIP-related tectonics (e.g. Maher 2001; Dostal & MacRae 2018). These changes in circulation may have brought cooler water-masses to regions bordering the Arctic, producing a decrease in local SSTs. Within the Chalk Sea and the Western Interior Seaway, rises in  $\delta^{13}\text{C}$  correlate with local transgressions (Voigt and Hillbrecht, 1997; Voigt and Wiese, 2000; Laurin et al., 2019). The timing of the cooling and circulation change observed in the Chalk Sea of

southern England is coincident with the rising limb of the P-CIE and evidence for a local transgression, suggesting deepening of the sea may have allowed an ingress of cooler boreal waters.



**Figure 9.** Potential models for cooling during the PCE.  $\delta^{13}\text{C}$  from Eastbourne (Tsikos et al., 2004). The gray box indicates the OAE 2 interval; the red box indicates the P-CIE; points 'a' to 'd' of the  $\delta^{13}\text{C}$  curve are labelled. The red lines indicate  $\text{CO}_2$ , the blue lines indicate SST, and the green line indicates circulation. Values are arbitrary. Model (1): a direct link between  $\text{CO}_2$ , atmospheric temperatures, and SSTs would produce a cooling interval after a drop in  $\text{CO}_2$ . Model (2): a fall in  $\text{CO}_2$  would drive global temperature decrease, forcing a circulation change and, in turn, further cooling. In this model, cooling must come after the  $\text{CO}_2$  change. Model (3):

no direct link between CO<sub>2</sub> and SSTs would produce variable timing and expression of temperatures at individual sites.

Although OAE 2 was a period of extreme global climate perturbation, the local temperature responses to increased CO<sub>2</sub> likely varied in magnitude, trend and, potentially, sign. Thus, interactions between climatic and oceanographic processes may account for the different expressions of cooling seen at different sites, especially the cooling seen in the early stages of the P-CIE. If nothing else, the apparent diachroneity in cooling highlights the problems associated with using any local expression of temperature or water-mass character during the Plenus interval as a correlation tool or stratigraphic marker.

## 5. Conclusions

The Cenomanian–Turonian transition experienced extreme climate change and major volcanic and tectonic activity. The increase in silicate weathering due to an enhanced hydrological cycle on the continents and the weathering of LIP-related basalts in the oceans probably drove a drawdown in CO<sub>2</sub>, as did high rates of organic-carbon burial. The on-going basalt–seawater interaction, likely concentrated in the first half of OAE 2 based on regional osmium-isotope signatures (Du Vivier et al., 2014, 2015), would have further affected both atmospheric *p*CO<sub>2</sub> and global carbon-isotope compositions. In contrast, volcanic outgassing and the cessation of organic-carbon deposition would have driven an *increase* in *p*CO<sub>2</sub>. However, it is not possible to disentangle these processes and their effects on the carbon cycle from the current data.

During the Plenus interval, there is evidence for widespread environmental change across the Northern Hemisphere. The global extent of negative  $\delta^{13}\text{C}$  excursions, coincident with records of increasing  $p\text{CO}_2$ , suggest an increase in atmospheric  $\text{CO}_2$  and a global carbon-cycle event—the Plenus CIE. However, the records of cooling show no consistency in timing or expression, and suggest either that some or all of the proxy records are compromised by diagenesis or environmental factors, and/or there was no clear-cut link between SSTs and atmospheric  $p\text{CO}_2$ . While there was likely a global fall in temperatures relating to the drop in  $\text{CO}_2$ , applying simple cause-and-effect relationships between  $\text{CO}_2$  and temperature does not explain all observations. Furthermore, variability in the timing and expression of changes in seawater chemistry, and problems in determining the driver of observed proxy changes, suggests that no one simple mechanism can link the carbon cycle to oceanography during the Plenus interval. While these stratigraphic offsets do not contradict the hypothesis of a global  $p\text{CO}_2$  decrease directly driving cooling with a concomitant or subsequent change in ocean circulation, they do suggest that local effects played a modifying role on the local timing and expression of events. To advance the understanding of the Plenus event, more geographically widespread records are required, ideally with proxies for temperature,  $\text{CO}_2$ , and ocean circulation applied in a single setting.

Given the global nature of the negative  $\delta^{13}\text{C}$  excursion and the decrease in atmospheric  $p\text{CO}_2$ , it is proposed that the Plenus CIE is a more reliable stratigraphic marker to identify the stratigraphic interval during which local expressions of the Plenus interval were developed with or without evidence for a fall in temperature and/or a drop in  $p\text{CO}_2$ .

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**Figure 1.** The composite ‘type-section’ recording OAE 2 and the Plenus Cold Event from the English Chalk, using  $\delta^{13}\text{C}_{\text{carb}}$  from Eastbourne (Tsikos et al., 2004), and bulk  $\delta^{18}\text{O}$  and boreal fauna from Dover (Lamolda et al., 1994; Gale and Christensen, 1996), correlated using the beds of the Plenus Marl Member (for details see Jarvis et al., 2006). Points ‘a–d’ show globally consistent positions on the  $\delta^{13}\text{C}$  curve (Jarvis et al., 2006). The gray box shows the interval of OAE 2 (Jenkyns et al., 2017) extending from the uppermost Cenomanian to the lowermost Turonian. The red bar indicates the Plenus carbon-isotope excursion, as defined in this study. The blue bars indicate cooling, with the upper bar defined in this study as the PCE *sensu stricto* (Gale and Christensen, 1996).

**Figure 2.** New geochemical data from the Plenus Marls at Dover, UK. Points ‘a’ and ‘b’ are identified on the  $\delta^{13}\text{C}$  curve. With the exception of  $\epsilon_{\text{Nd}}$ , error bars are smaller than the data points. The red dotted line indicates the onset of OAE 2; the red bar indicates the Plenus carbon-isotope excursion; the blue bar indicates the PCE *sensu stricto*.

**Figure 3.** Global distribution of known records demonstrating the Plenus CIE (a negative  $\delta^{13}\text{C}$  excursion between points ‘a’ and ‘b’ in Figure 1) or an excursion in  $\text{CO}_2$  across the Plenus interval, as indicated by  $\Delta^{13}\text{C}$ , compound-specific  $\delta^{13}\text{C}$ , or leaf stomata. **1** Pratt’s Landing (van Helmond et al., 2016); Vermillion River, Well 10-35-45-2WA (Prokoph et al., 2013). **2** Cuba, KS (Bowman & Bralower 2015); Pueblo (Barclay et al., 2010; Bowman & Bralower, 2005; Caron et al., 2006; Keller et al., 2008; Pratt et al., 1985; Sageman et al., 2006); USGS Portland-1 core (Eldrett et al., 2017); Aristocrat Angus core (Joo and Sageman, 2014); Hot Springs, CO (Desmares et al., 2007); SH#1 core (Jones et al., 2019); generalized Western Interior Seaway

1352 (Orth et al., 1993). **3** Great Valley Sequence, CA (Du Vivier et al., 2015). **4** Innes-1 core, Iona-1  
1353 core, Well X core (Eldrett et al., 2017). **5** Axaxacoalco, Barranca el Tigre, Barranco el Canon  
1354 (Elrick et al., 2009). **6** Laurichocha, Piedra Parada, Uchucchacua (Navarro-Ramirez et al., 2016,  
1355 2017). **7** Bass River, NJ (Bowman and Bralower, 2005; van Helmond et al., 2013). **8** ODP Site  
1356 1258 (Erbacher et al., 2005); ODP Site 1260 (Eldrett et al., 2017; Erbacher et al., 2005; Forster et  
1357 al., 2007; van Bentum et al., 2012); ODP Site 1261 (Eldrett et al., 2017; Erbacher et al., 2005). **9**  
1358 DSDP Site 367 (Dickson et al., 2016; Forster et al., 2007; Kuypers et al., 1999; Sinninghe  
1359 Damsté et al., 2008). **10** Tarfaya (Keller et al., 2008; Kolonic et al., 2005; Kuhnt et al., 2017;  
1360 Kuypers et al., 2002; Tsikos et al., 2004); Mpl, S57, S75 (Kolonic et al., 2005); S13 (Kuypers et  
1361 al., 1999; Kolonic et al., 2005). **11** ODP Site 1276 (Sinninghe Damsté et al., 2008; van Helmond  
1362 et al., 2014). **12** Arobes, Ganuza, Menoyo (Kaiho et al., 2014); Manilvala (Mort et al., 2007);  
1363 Puentedey (Barroso-Barcenilla et al., 2011). **13** Dover (this study; Jeans et al., 1991; Lamolda et  
1364 al., 1994); Eastbourne (Jenkyns et al., 1994; Paul et al., 1999; Tsikos et al., 2004; Gale et al.,  
1365 2005; Pearce et al., 2009; Zheng et al., 2013); Culver Cliff (Jarvis et al., 2001). **14** Gröbern  
1366 (Voigt et al., 2006); Halle (Voigt et al., 2007); Wunstorf (Voigt et al., 2008; Du Vivier et al.,  
1367 2014); Roter Sattel (Charbonnier et al., 2018). **15** Lambruisse (Takashima et al., 2009); Pont  
1368 d'Issole (Grosheny et al., 2006; Jarvis et al., 2011); les Lattes, Le Bourgeut (Grosheny et al.,  
1369 2017); Cassis (Heimhofer et al., 2018); Clot Chevalier (Gale et al., 2019). **16** Pecínov, Czech  
1370 Republic (Košťák et al., 2017). **17** Bottaccione (Kuroda et al., 2007); Furlo (Mort et al., 2007);  
1371 Gubbio (Jenkyns et al., 1994; Tsikos et al., 2004); Raia del Pedale (Owens et al., 2013); Monte  
1372 Coccovello, Monte Varchera (Parente et al., 2008). **18** Crimea (Fisher et al., 2005). **19** Jerissa  
1373 (Zaghib-Turki & Soua 2013); Oued Mellegue (Nederbragt & Fiorentino 1999); Wadi Bahoul  
1374 (Caron et al., 2006). **20** Wadi Feiran (El-Sabbagh et al., 2011). **21** Ghawr Al Mazar (Wendler et

al., 2016); Wadi Karak (Farouk et al., 2017). **22** Aimaki, Khadzhalmakhi, Levashi (Gavrilov et al., 2013). **23** Taherabad (Kalanat et al., 2018). **24** Tappu (Nemoto & Hasegawa 2011); Yezo (Du Vivier et al., 2015). **25** ODP Site 530 (Forster et al., 2008). **26** Gongzha (Bomou et al., 2013); Tingri (Li et al., 2006). **27** Sawpit Gully, Mangaotane B (Hasegawa et al., 2013; Gangl et al., 2019); Mangaotane A (Hasegawa et al., 2013).

**Figure 4.** Comparison of  $\delta^{13}\text{C}_{\text{org}}$  and  $\delta^{13}\text{C}_{\text{hopane}}$  records from ODP Site 1276, Cape Verde Basin (adapted from Sinninghe Damsté et al., 2010) demonstrating a stratigraphic offset in the position of the negative excursion seen in  $\delta^{13}\text{C}_{\text{org}}$  at ~1083.1 mbsf and in  $\delta^{13}\text{C}_{\text{hopane}}$  at ~1082.8 mbsf.

**Figure 5.** Records of  $\text{CO}_2$  change across the Plenus interval. The gray boxes indicate the OAE 2 interval; the red boxes indicate the P-CIE; the blue boxes indicate the PCE *sensu stricto*; points ‘a’ to ‘c’ of the OAE are labelled. Coloured bands illustrate visual approximations of trends.

**Figure 6.** Global distribution of known records demonstrating a change in temperature across the PCE interval, based on records of  $\text{TEX}_{86}$ ,  $\delta^{18}\text{O}$ , faunal assemblages, and foraminiferal coiling. **1** Pratt’s Landing (van Helmond et al., 2016). **2** Hot Springs, SD (Desmares et al., 2016); Pueblo (Caron et al., 2006; Desmares et al., 2016); USGS Portland-1 Core (Eldrett et al., 2017). **3** Iona-1 core, Innes-1 core, Well X core (Eldrett et al., 2017). **4** Bass River, NJ (van Helmond et al., 2013). **5** ODP Site 1260 (Forster et al., 2007; Eldrett et al., 2017). **6** DSDP Site 367 (Forster et al., 2007). **7** Tarfaya (Tsikos et al., 2004; Kuhnt et al., 2017). **8** ODP Site 1276 (Sinninghe Damsté et al., 2008). **9** Arobes, Ganuza, Menoyo (Kaiho et al., 2014); Puentedey (Barroso-

Barcenilla et al., 2011). **10** Dover (this study; Jefferies 1962; Jeans et al., 1991; Lamolda et al.,  
1994); Eastbourne (Jenkyns et al., 1994; Paul et al., 1999; Tsikos et al., 2004; Voigt et al., 2004,  
2006; Pearce et al., 2009; Zheng et al., 2013). **11** Gröbern (Voigt et al., 2006); Halle (Voigt et al.,  
2007); Wunstorf (van Helmond et al., 2015). **12** Cassis (Heimhofer et al., 2018); Clot Chevalier  
(Gale et al., 2019); Lambruisse (Takashima et al., 2009); les Lettes (Gale & Christensen 1996);  
Pont d'Issole (Jarvis et al., 2011). **13** Gubbio (Jenkyns et al., 1994). **14** Crimea (Fisher et al.,  
2005). **15** Oued Mellegue (Nederbragt & Fiorentino 1999); Wadi Bahoul (Caron et al., 2006). **16**  
Wadi Karak (Farouk et al., 2017). **17** Amaki, Khadzhalmakhi, Levashi (Gavrilov et al., 2013). **18**  
Taherabad (Kalanat et al., 2018).

**Figure 7.** Records of SSTs during the Plenus interval. The gray boxes indicate the OAE 2  
interval; the red boxes indicate the P-CIE; the blue boxes indicate the PCE *sensu stricto*; points  
'a' to 'c' of the OAE are labelled. Dover stratigraphy from Lamolda et al., 1994; Wunstorf  
stratigraphy from Voigt et al., 2008. Coloured bands illustrate visual approximations of trends.

**Figure 8.** Global distribution of known records demonstrating a change in water-mass character  
across the Plenus interval, as indicated by elemental, isotopic, lithological, or faunal changes in  
the sedimentary record. **1** Vermillion River (Prokoph et al., 2013). **2** Angus Aristocrat core  
(Zhou et al., 2015); Cuba, KS (Bowman & Bralower 2015; Elderbak et al., 2014); Hot Springs,  
SD (Desmares et al., 2016); USGS Portland-1 core (Du Vivier et al., 2014; Holmden et al., 2016;  
Eldrett et al., 2017); generalized Western Interior Seaway (Orth et al., 1993); Pueblo (Bowman  
& Bralower, 2005; Caron et al., 2006; Keller et al., 2008; Elderbak et al., 2014). **3** Great Valley  
Sequence, CA (Du Vivier et al., 2015). **4** Innes-1 core, Iona-1 core, Well X core (Eldrett et al.,

2017). **5** Barranco el Canon (Elrick et al., 2009; Sweere et al., 2018). **6** Bass River, NJ (Bowman  
 and Bralower, 2005). **7** ODP Site 1258 (Erbacher et al., 2005; Friedrich et al., 2006; Ostrander et  
 al., 2017; Zhou et al., 2015); ODP Site 1260 (Erbacher et al., 2005; Friedrich et al., 2006; Forster  
 et al., 2007; Turgeon and Creaser, 2008; Du Vivier et al., 2014; Eldrett et al., 2017); ODP Site  
 1261 (Erbacher et al., 2005; Friedrich et al., 2006). **8** DSDP Site 367 (Kuypers et al., 1999;  
 Forster et al., 2007, 2008; Sinninghe Damsté et al., 2008; Du Vivier et al., 2014; Dickson et al.,  
 2016). **9** Tarfaya (Kuypers et al., 2002; Tsikos et al., 2004; Keller et al., 2008; Dickson et al.,  
 2016; Kuhnt et al., 2017); Mpl, S13, S57, S75 (Kolonic et al., 2005). **10** ODP Site 1276  
 (Sinninghe Damsté et al., 2008; van Helmond et al., 2014). **11** Puentevedey (Barroso-Barcenilla et  
 al., 2011); Arobes (Kaiho et al., 2014); Ganuza (Peryt and Lamolda, 1995; Kaiho et al., 2014);  
 Manivala (Mort et al., 2007); Menoyo (Peryt and Lamolda, 1995; Kaiho et al., 2014). **12** Dover  
 (this study; Jeans et al., 1991); Eastbourne (Orth et al., 1993; Paul et al., 1999; Pearce et al.,  
 2009; Lu et al., 2010; Owens et al., 2013; Zheng et al., 2013; Zhou et al., 2015; Clarkson et al.,  
 2018; Sweere et al., 2018). **13** Wunstorf (van Helmond et al., 2015); Halle (Voigt et al., 2007);  
 Roter Sattel (Charbonnier et al., 2018); Wunstorf (Du Vivier et al., 2014; van Helmond et al.,  
 2015). **14** Clot Chevalier (Gale et al., 2019); Lambruisse (Takashima et al., 2009); Le Bourgeut  
 (Grosheny et al., 2017); Pont d'Issole (Grosheny et al., 2006; Jarvis et al., 2011; Danzelle et al.,  
 2018); Vocontian Basin (Du Vivier et al., 2014). **15** Bottaccione (Kuroda et al., 2007); Furlo  
 (Mort et al., 2007); Gubbio (Tsikos et al., 2004); Raia del Pedale (Owens et al., 2013; Zhou et  
 al., 2015; Clarkson et al., 2018; Sweere et al., 2018). **16** Crimea (Fisher et al., 2005). **17** Oued  
 Mellegue (Nederbragt & Fiorentino 1999); Wadi Bahoul (Caron et al., 2006). **18** Wadi Feiran  
 (El-Sabbagh et al., 2011). **19** Wadi Karak (Farouk et al., 2018). **20** Aimaki, Khadzhamkhi,  
 Levashi (Gavrilov et al., 2013). **21** Gharesu (Kalanat et al., 2016); Taherabad (Kalanat et al.,

2016, 2017). **22** Tappu (Nemoto & Hasegawa 2011); Yezo Group (Du Vivier et al., 2015). **23**  
DSDP Site 530 (Forster et al., 2008; Du Vivier et al., 2014). **24** Gongzha (Bomou et al., 2013).

**Figure 9.** Potential models for cooling during the PCE.  $\delta^{13}\text{C}$  from Eastbourne (Tsikos et al.,  
2004). The gray box indicates the OAE 2 interval; the red box indicates the P-CIE; points ‘a’ to  
‘d’ of the  $\delta^{13}\text{C}$  curve are labelled. The red lines indicate  $\text{CO}_2$ , the blue lines indicate SST, and the  
green line indicates circulation. Values are arbitrary. Model (1): a direct link between  $\text{CO}_2$ ,  
atmospheric temperatures, and SSTs would produce a cooling interval after a drop in  $\text{CO}_2$ .  
Model (2): a fall in  $\text{CO}_2$  would drive global temperature decrease, forcing a circulation change  
and, in turn, further cooling. In this model, cooling must come after the  $\text{CO}_2$  change. Model (3):  
no direct link between  $\text{CO}_2$  and SSTs would produce variable timing and expression of  
temperatures at individual sites.